PB-221 513

DEVELOPMENT OF DISSOLVED OXYGEN CRITERIA FOR FRESHWATER FISH

OREGON STATE UNIVERSITY

FEBRUARY 1973

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EPA-R3-73-019
FEBRUARY 1973

W73-11327

Ecological Research Series

PB 221 513

DEVELOPMENT OF DISSOLVED OXYGEN CRITERIA FOR FRESHWATER FISH

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1 Accession Number W 73-11327	2 Subject Field & Group 05C	**SELECTED WATER RESOURCES ABSTRACTS** **INPUT TRANSACTION FORM**

5 Organization
Oregon State University, Corvallis, Oregon,
Department of Fisheries and Wildlife.

6 Title
DEVELOPMENT OF DISSOLVED OXYGEN CRITERIA FOR FRESHWATER FISH,

10 Author(s)
C~~harles~~ E. Warren,
P~~eter~~ Doudoroff, and
D~~ean~~ L. Shumway

16 Project Designation
EPA Pro~~gram~~ject #18050 DJZ

~~21~~ ~~Note~~ 22
Environmental Protection Agency, report ~~number,~~ EPA-R3-73-019, February 1973. 121p, Ecological Research Series

~~22 Citation Warren, Charles E. (Principal Investigator) 1971. Development of dissolved oxygen criteria for freshwater fish. Terminal Report from Department Fisheries and Wildlife, Oregon State University, Corvallis to U.S. Environmental Protection Agency Washington D.C. (EPA Program #18050DJZ~~

23 Descriptors (Starred First)
*Oxygen requirements, *Fish, *Fish growth, *Fish respiration, *Fish reproduction, Salmon, Trout, Bass, Pollution (water), Aquatic productivity, Water quality, *Dissolved oxygen, Water pollution effects

25 Identifiers (Starred First)
*Pacific salmon, *Steelhead trout, *Largemouth bass. *Laboratory studies, ~~and oxygen requirements of fish~~.

27 Abstract
~~The~~ research ~~here reported~~ has involved laboratory studies on the survival, development, bioenergetics and growth, swimming performance, and avoidance behavior of chinook and coho salmon, steelhead trout, and largemouth bass. Some ~~of the~~ studies have been conducted under very simple laboratory conditions, as in aquaria or other apparatus, but some ~~of the~~ studies on bioenergetics and growth have also been conducted under rather natural conditions in laboratory streams and ponds. In some important cases, ~~we have found~~ close correspondence was found between the effects of reduced oxygen concentration in aquarium studies of growth at maximum rations and its effects under more natural conditions in laboratory streams and ponds. Some of the biological responses of the fish studies were affected by any appreciable reduction in dissolved oxygen below the air saturation levels, whereas others were affected only at levels below about 50 percent the air saturation levels. (EPA)

21) Copy available from GPO Sup Doc as 123:73/019, \$2.10; microfiche from NTIS as PB 221 513, \$0.95.

NTIS \$4.60

Abstractor Charles E. Warren	Institution Oregon State University

WR:102 (REV. JULY 1969)
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☆ GPO: 1970-389-930

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EPA-R3-73-019
February 1973

DEVELOPMENT OF DISSOLVED OXYGEN CRITERIA FOR FRESHWATER FISH

By

Charles E. Warren
Peter Doudoroff
Dean L. Shumway
Oregon State University, Corvallis, OR

Project 18050 DJZ

Project Officer

Dr. Gerald R. Bouck
Western Fish Toxicology Laboratory
200 South 35th Street
Corvallis, Oregon 97330

Prepared for

OFFICE OF RESEARCH AND MONITORING
U.S. ENVIRONMENTAL PROTECTION AGENCY
WASHINGTON, D.C. 20460

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402
Price $2.10 domestic postpaid or $1.75 GPO Bookstore

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EPA Review Notice

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ABSTRACT

This terminal report nominally covers laboratory research on the dissolved oxygen requirements of salmonid and centrarchid fishes conducted from September 1, 1968 through August 31, 1971. But because our interpretation of the results of this research, our conclusions, and our recommendations are to a considerable extent based on the results of research we conducted from September 1, 1955 through August 31, 1968, we have included a summary of this earlier work.

The research here reported has involved laboratory studies on the survival, development, bioenergetics and growth, swimming performance, and avoidance behavior of chinook and coho salmon, steelhead trout, and largemouth bass. Some of the studies have been conducted under very simple laboratory conditions, as in aquaria or other apparatus, but some of the studies on bioenergetics and growth have also been conducted under rather natural conditions in laboratory streams and ponds. In some important cases, we have found close correspondence between the effects of reduced oxygen concentration in aquarium studies of growth at maximum rations and its effects under more natural conditions in laboratory streams and ponds.

Some of the biological responses of the fish studies were affected by any appreciable reduction in dissolved oxygen below the air saturation levels, whereas others were affected only at levels below about 50 percent the air saturation levels.

This report was submitted in fulfillment of Grant No. 18050 DJZ between the Environmental Protection Agency and Oregon State University.

Key Words: Oxygen standards, oxygen requirements of fish, Pacific salmon, steelhead trout, largemouth bass.

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CONCLUSIONS

1. Under laboratory conditions, the juvenile centrarchids and salmonids tested were usually capable of surviving for indefinite, prolonged periods of time at dissolved oxygen concentrations as low as 2 mg/l and less, except at relatively high temperatures.

2. Under certain laboratory conditions, juvenile centrarchids and salmonids were capable of avoiding low oxygen concentrations well above lethal levels, but these fish did not avoid some higher concentrations that have been shown to have adverse sublethal effects.

3. Any considerable reduction of dissolved oxygen concentration from the air-saturation level resulted in some reduction of the maximum sustained swimming speeds of juvenile coho and chinook salmon at temperatures between 10 and 20C; juvenile largemouth bass were so affected only by reductions of dissolved oxygen to levels below 5 or 6 mg/l at 25C.

4. Any reduction from the air-saturation level of the dissolved oxygen concentration to which embryos of coho and chinook salmon and steelhead trout were exposed throughout their development resulted in some reduction in size of the hatching fry and some delay of hatching, but the percentage of embryos hatching at normal temperatures was demonstrably impaired under the experimental conditions in the laboratory only at levels below 3 mg/l; the size of the hatching fry was a function also of water velocity and increased with increase of water velocity.

5. The maximum sizes attained by salmonid fry of different species at the time of complete absorption of the yolk sacs were often reduced, in varying degrees, by reduction of the oxygen concentration to which the alevins were exposed, but this effect was never nearly as pronounced as was the reduction in initial size of fry hatching from eggs exposed continuously to the same low oxygen concentration.

6. Increase of carbon dioxide concentration to levels likely to occur in waters whose oxygen content is moderately reduced by decomposition of organic matter had little or no effect on the resistance to low oxygen concentrations, on the swimming ability, and on the embryonic development of fish species tested; furthermore, effects of higher carbon dioxide concentrations on the maximum sustained swimming speeds of juvenile coho salmon were much less pronounced at very low oxygen concentrations than at high oxygen concentrations; acclimation to high levels of free carbon dioxide was found to be rapid.

7. Except at relatively low temperatures, any considerable reduction of dissolved oxygen from air-saturation levels usually resulted in some reduction of the food consumption and growth rates of juvenile coho and chinook salmon and largemouth bass provided with unrestricted food

rations in laboratory aquaria; when rations were uniformly restricted and small, the growth of coho salmon was not so affected, except perhaps at very low levels of dissolved oxygen.

8. When food rations were unrestricted, wide fluctuations of dissolved oxygen between very low and high levels had an adverse effect on the growth of both coho salmon and largemouth bass, the impairment of growth being as great as that caused by continuous exposure of the fish to low oxygen concentrations not far above the low levels to which the fish subjected to the fluctuating concentrations had been exposed.

9. The dependence of the food consumption and growth of largemouth bass in laboratory aquaria on dissolved oxygen concentrations above very low levels disappeared abruptly with reduction of temperature from 20 to 15C; coho and chinook salmon showed a less pronounced temperature effect, or a more gradual decline of the critical level of dissolved oxygen with reduction of temperature.

10. In artificial ponds at moderately high temperatures, the growth rates of juvenile largemouth bass feeding more or less naturally on mosquitofish were dependent on the availability of the food, yet were reduced by reduction of the oxygen concentration about as much as were the growth rates of bass in aquarium tests in which rations were unrestricted and growth was much more rapid than it was in the ponds. The noted agreement between the results of the pond and aquarium tests, as well as other related data and bioenergetic (energy-balance) computations, indicate that the metabolic rates of the bass in the ponds are high and virtually independent of food-organism density, their activity increasing as food availability, food intake, and the specific dynamic action of the food decrease.

11. As in aquarium experiments, the growth of juvenile chinook salmon held in laboratory streams at 9-13C and feeding on organisms produced in these streams was reduced by reductions of oxygen concentration from the air-saturation level, when food availability and growth rates were relatively high; they were virtually independent of oxygen concentration when food availability and growth rates were low. In view of the apparent dependence of the critical dissolved oxygen levels upon food availability and intake in the laboratory streams, close correspondence of the effects of dissolved oxygen reduction on the growth of salmon in the streams and in laboratory aquaria with unlimited food cannot be assumed, particularly when temperatures are high.

12. Although adverse effects of reduced oxygen concentrations on embryonic survival and growth sometimes may result in serious reduction of fish production, only the effects on growth rates, determined experimentally, can now be reasonably relied upon in arriving at estimates of maximum reductions of oxygen concentration that would result in impairment (percent reduction) of fish production in nature not exceeding some particular degree of impairment that may be deemed

acceptable. Such estimates may be useful in arriving at water quality standards intended for the protection of the natural production of particular species of fish.

SUMMARY OF RECOMMENDATIONS

1. If dissolved oxygen criteria are to be adopted for wide (e.g., nationwide or worldwide) application in the protection of freshwater fisheries in general, the adoption of criteria proposed by Doudoroff and Shumway (1970) is recommended. These criteria (see Appendix III for full details) are based on the pertinent world literature. They are in the form of curves relating "acceptable" dissolved oxygen minima deemed compatible with each of several different levels of protection of fisheries to the estimated natural seasonal minima for the waters to which the criteria apply, in a given season of the year.

2. If, on the other hand, the criteria adopted are to be designed for the protection of the production of particular species of fish and based on the assumption that the degree of impairment of this production at reduced oxygen concentrations is adequately indicated by the reduction of growth rates of the fish under experimental conditions when rations are unrestricted, the following criteria (acceptable dissolved oxygen minima) pertaining to largemouth bass and coho salmon (the species emphasized in our studies) are recommended:

A. If no reduction of production rates from the rates possible at high (near-saturation) levels of dissolved oxygen is to be accepted as permissible at any time:

(1) For largemouth bass, no reduction of dissolved oxygen concentration from the high levels at temperatures above 15C, and a minimum concentration of 4.2 mg/l at temperatures near and below 15C.

(2) For coho salmon, no reduction of dissolved oxygen concentration from the high levels at any temperature.

B. If only a 10 percent reduction of production rates from the rates possible at high oxygen concentrations is to be deemed the maximum acceptable reduction at any time:

(1) For largemouth bass, minimum dissolved oxygen concentrations of 3 mg/l at temperatures near and below 15C, and 5 mg/l at temperatures near and above 20C.

(2) For coho salmon, 5 mg/l, except at unusually high temperatures, near 22C, at which a minimum requirement of 5.5 or 6 mg/l is indicated.

C. If a 20 percent reduction of production rates from the rates possible at high (near-saturation) levels of dissolved oxygen is to be deemed the maximum acceptable reduction at any time:

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(1) For largemouth bass, minimum dissolved oxygen concentrations of 2.5 mg/l at temperatures near and below 15C and 4 mg/l at temperatures near and above 20C.

(2) For coho salmon, about 4 mg/l, except at unusually high temperatures, near 22C, at which a minimum requirement of 5 mg/l is indicated.

The rationale of these proposed criteria is fully explained and assumptions on which they are based are critically examined in the section of this report entitled "Suggestions Concerning Water Quality Criteria for Protection of Fisheries." It is pointed out there that, although dissolved oxygen minima in streams where coho salmon spawn are not likely to occur when coho salmon embryos or larvae are present, effects of reduced oxygen concentrations in these streams on coho salmon reproduction may often be more important or critical than the effects on juvenile growth, because, among other reasons, oxygen concentrations in water percolating through streambed gravels where coho salmon eggs are deposited are often much lower than those in water flowing over the gravels.

GENERAL INTRODUCTION

There will continue to be a very real need for information on the dissolved oxygen requirements of fish, so long as there is concern for the protection of fisheries by means of water quality standards. And in any period of time, regardless of the information available, there is and will be the problem of just how this laboratory and other information is to be interpreted in order to determine reliable dissolved oxygen standards that are adequate to protect fishery resources in natural waters. And still further, there is always the problem of identifying the most important research remaining to be pursued, for there are limitations of time, talent, and money that we must face in pursuit of our pollution control objectives. This report presents a rather substantial amount of information on the dissolved oxygen requirements of several species of freshwater fish, as determined under laboratory conditions. But it goes beyond the ordinary limits of such research reports to include various materials--as will be explained--that seem to us to be necessary in maximizing the value of existing information and future research for water pollution control.

This terminal report nominally covers the methods, results, and interpretation of research we have conducted from September 1, 1968 through August 31, 1971, on the dissolved oxygen requirements of freshwater fishes. But the interpretation of these results and recommendations as to dissolved oxygen standards and research yet needed derive to a considerable extent from the results of research we conducted during the period from September 1, 1955 through August 31, 1968, with support from predecessor agencies of the Environmental Protection Agency. Thus, we have included in this report a general summary of the results and interpretation of this earlier research. Whereas the results of the more recent research are presented in considerable detail in text figures and appendix tables (Appendix IV), no figures or tables are included for the earlier work, which has been already reported in detail in the publications and theses listed in Appendix I. Nearly all literature citations in the body of this report can be found in Appendix I. All others are given in footnotes.

After major sections on recent research and earlier research, there follows a discussion of the possible significance of our laboratory results as these may relate to the oxygen requirements of fish in their natural environments. Next in sequence are major sections in which we make suggestions concerning water quality criteria for the protection of fisheries and recommendations for future research on the dissolved oxygen requirements of fishes.

Knowledgeable biologists often disagree strongly as to the kinds of research most needed. This is in part because of their different backgrounds and the different importances they assign to various environmental factors and responses of the animals. But much of such disagreement derives from failure to identify alternative assumptions or propositions crucial to consideration of the problem. Once this has been done, one can logically deduce, for any set of assumptions, the research most necessary to resolve the problem. We have attempted in Appendix II to develop a logical scheme for identifying, given different assumptions, the kinds of research most needed. This sort of approach should prove of value not only in planning research but also in setting standards, as it will identify the assumptions involved in either case. It should prove of value in considering not only oxygen problems but also other kinds of pollution problems.

The matter of setting standards poses several dilemmas. As indicated above, we have included in the body of this report some suggestions on this problem. In addition, in Appendix III, we have reprinted--with permission of FAO--a scheme Doudoroff and Shumway (1970) proposed for setting oxygen standards. We are not recommending this scheme, which like any scheme has difficulties. But we do believe that those concerned with water quality regulation should give it careful attention, because it represents one of the few viable alternatives for setting oxygen standards for the protection of fisheries.

METHODS, RESULTS, AND INTERPRETATION OF RESEARCH CONDUCTED FROM SEPTEMBER 1, 1968 THROUGH AUGUST 31, 1971, ON THE BIOENERGETICS AND GROWTH OF SALMON AND LARGEMOUTH BASS IN AQUARIA, RESPIRATION CHAMBERS, EXPERIMENTAL PONDS, AND LABORATORY STREAMS

INTRODUCTION

The presentation in this major part of this report covers the methods, results, and interpretation of research we have conducted during the past three years, September 1, 1968 through August 31, 1971, the period nominally covered by this terminal report. As indicated in the general introduction to the overall report, however, we will, in the major part following this one, include a general summary of our research on the oxygen requirements of fish for the period September 1, 1955 through August 31, 1968. But consideration of research conducted during the past three years will be in greater detail than consideration of the earlier research. We are doing this because this report is nominally for the past three years of research, the earlier research has been previously reported in detailed progress reports and publications, and because the procedures of the past three years have led to results that are in some ways more easily interpreted with regard to the oxygen requirements of freshwater fish in nature.

This present major part of this report will be presented in four sections: Aquarium Studies of Bioenergetics and Growth of Salmon and Largemouth Bass as Influenced by Dissolved Oxygen Concentration; Respiration Chambers and other Studies of Bioenergetics and Growth of Coho Salmon as Influenced by Dissolved Oxygen Concentration; Experimental Pond Studies of the Bioenergetics and Growth of Largemouth Bass as Influenced by Dissolved Oxygen Concentration; and Laboratory Stream Studies of the Growth of Chinook Salmon as Influenced by Food Density and Dissolved Oxygen Concentration. Because the methods employed by research presented in each of these four sections are in some ways peculiar to that research, a methods subsection will be included in each of these four sections.

AQUARIUM STUDIES OF BIOENERGETICS AND GROWTH OF SALMON AND LARGEMOUTH BASS AS INFLUENCED BY DISSOLVED OXYGEN CONCENTRATION

Experimental Apparatus, Materials, and Procedures

Experimental Apparatus

The purpose of the apparatus used in this investigation was to provide measured flows of water of controlled temperature and dissolved oxygen concentration to a series of sealed chambers containing test fish. The two identically constructed and independently operated sets of experimental gear, each containing six test chambers, were located in a constant-temperature room, provided with filtered water from a small springfed stream, and illuminated 16 hours daily by timer-controlled fluorescent lights. Pyrex glass bottles, each having a capacity of 45 liters, were used as test chambers. This apparatus was similar to apparatus used by Herrmann, et al. (1962), Fisher (1963), and Stewart et al. (1967). One set of six test chambers and associated control equipment is shown in Figure 1.

Water from the main supply was distributed from two constant-level headboxes to the two sets of experimental chambers. In the headboxes, incoming water was vigorously aerated with compressed air and heated to the desired temperature by a thermostatically controlled stainless-steel immersion heater. From each headbox, warmed water passed through tygon plastic tubing into six columns constructed of 50 mm ID glass pipe. Water entered each column through a glass tube inserted through the stoppered base and extending to its upper one-third. Water of the desired oxygen concentration left each column near the base and passed through a flow-adjustment stopcock, a ball-displacement flowmeter, and a 250 ml BOD bottle used for water sample collection, and into the test chamber at a rate of near 300 ml/min, through a glass tube inserted through the stopper and extending to near the bottom of the test chamber. After flowing out through a glass tube extending into the neck of the test vessel, the water passed through a second 250 ml BOD bottle and was discharged from the system via the floor drain.

Compressed oxygen and nitrogen gases were used to obtain the desired dissolved oxygen concentrations in the water leaving the glass columns. Two-stage pressure regulators were used to control the discharge of gases from the compressed gas cylinders into a gas manifold constructed of threaded and capped steel pipe tapped with brass gas valves. Two such manifolds were used, one for oxygen and one for nitrogen. Gas from the manifold flowed through one of twelve ball-displacement gas flowmeters and entered each glass column, where it was dispersed into bubbles by an aquarium airstone placed near the base. The gas bubbles streamed upward to form a counterflow to the downward flow of water and effectively brought oxygen concentrations to the desired levels.

Experimental Materials

The fish tested in these experiments were juvenile largemouth bass seined from ponds in the Willamette Valley, juvenile coho salmon seined from the upper Yaquina River near Nashville, and juvenile chinook salmon seined from the Sixes River located on the southern Oregon coast.

Once obtained, the stocks of fish used in experiments were held in a continuously illuminated, 189-liter aquarium at near the test temperature and fed a diet of live food organisms. Largemouth bass were fed large quantities of salmonid fry and tubificid worms; coho and chinook salmon were provided tubificid worms only. The test fish were held under these conditions for a minimum of one week prior to their removal and use in experiments.

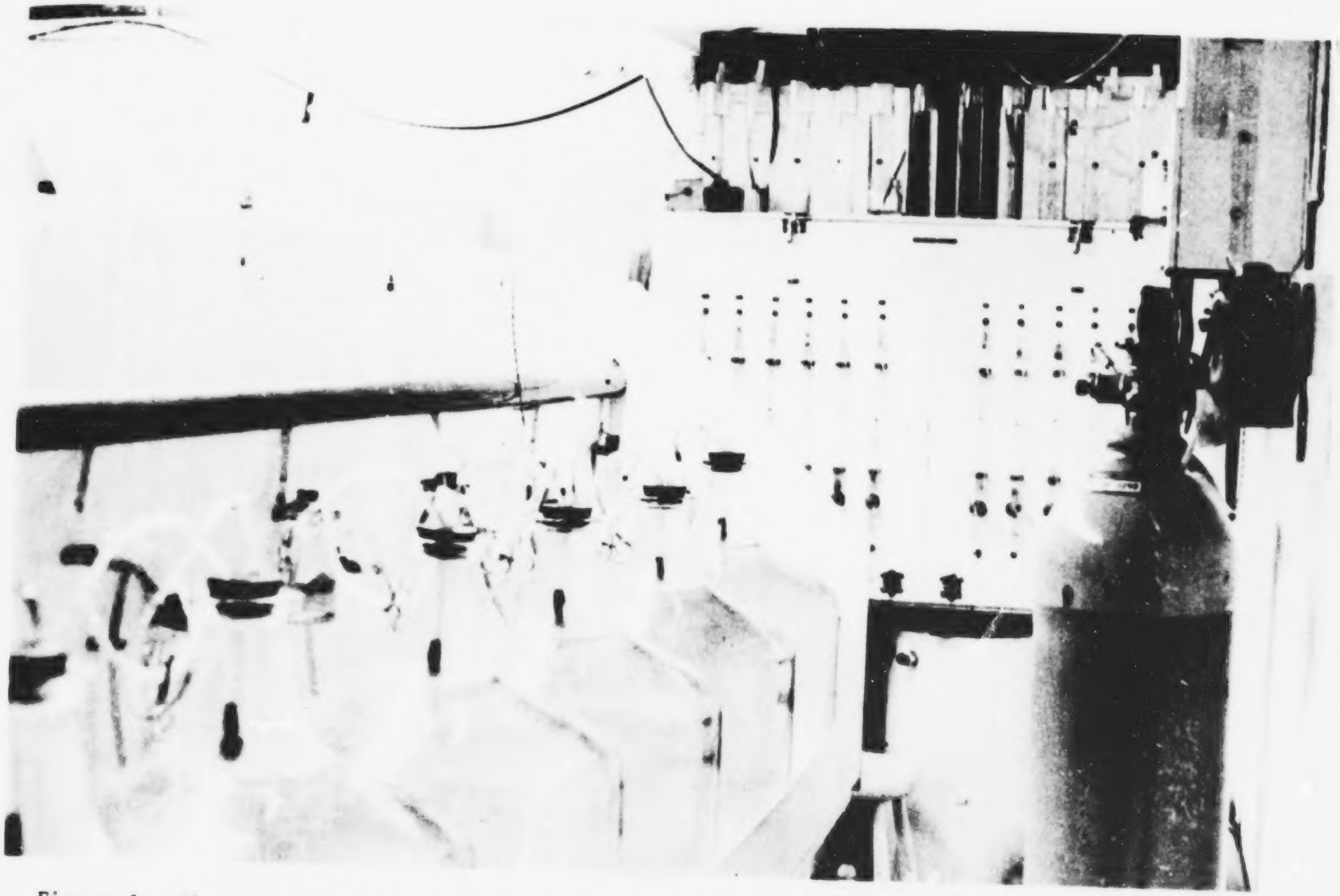

Figure 1. Photograph showing one of the two sets of vessels used for growth in this study.

Salmonid fry used as food for largemouth bass were either chinook salmon or coho salmon obtained as fry, or were steelhead trout obtained as eggs, which were then incubated, hatched, and reared to the desired size. The salmonid fry and eggs were obtained from various hatcheries operated by the Oregon State Game Commission or the Fish Commission of Oregon. The fry were held in outdoor tanks and fed Oregon Moist Pellet.

Tubificid worms used as food were obtained from the Roaring River Trout Hatchery of the Oregon State Game Commission. These worms were held in outdoor troughs prior to use as food organisms.

Experimental Procedures

Four days prior to the start of each experiment, about one-half the available stock of fish was removed from the 189-liter aquarium and sorted into seven groups of an appropriate number of fish of nearly equal size. In most experiments, the fish in each group were lightly anesthetized with tricane methanesulphonate (MS 222), individually marked by the cold branding technique described by Ellis (1968)*, weighed, and measured. In other experiments, the fish were not individually marked. All weights taken during the study were recorded to the nearest 0.01 g and lenths to the nearest 1.0 mm, unless otherwise stated.

Prior to the start of an experiment, six of the seven groups of test fish were introduced into the experimental apparatus and held for four days at dissolved oxygen concentrations near to those at which they were to be tested. The seventh group of fish was placed in a small aquarium and held for the same period of time at near the air-saturation level of oxygen. All seven groups of fish were held at the selected test temperature during the four-day adjustment period. Test fish were fed daily a near-maintenance ration of food; all seven groups of fish received the same amount of food each day. With the exception of one group in each experiment with largemouth bass, salmonid fry were used as food organisms in the test with largemouth bass, and tubificid worms were used as food for the salmonids. The excepted group of largemouth bass were fed tubificid worms. Test fish were not fed for 24 hours prior to the start of each experiment. This allowed for the elimination of most of the food and fecal material from their digestive tract before they were reweighed.

At the start of each experiment, the groups of fish acclimated for four days were removed from the test vessels and aquarium and lightly anesthetized with MS 222. They were then individually weighed and measured. The extra group of fish from the aquarium was dried to a constant weight in an oven at 70C for determination of the ration of dry weight to wet weight. This ratio was used in computing the initial dry weight of all fish used in that experiment.

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* Ellis, R. H. 1968. Effects of kraft pulp mill effluent on the production and food relations of juvenile chinook salmon in laboratory streams. M.S. Thesis. Oregon State University, Corvallis. 55p.

The test fish were fed shortly after being returned to the test vessels. With the exception of three experiments with chinook salmon, the rations provided exceeded by a small margin the maximal amount of food that could be consumed by the fish during a 24-hr period and are termed unrestricted rations, according to the definition of Doudoroff and Shumway (1970). In the excepted tests, restricted rations were provided the chinook salmon five out of seven days; on the other two days of each week, unrestricted rations were provided. The test fish were normally fed each day in the morning.

In order to maintain the desired experimental conditions, it was necessary to check the apparatus twice each day between 7:00 and 9:00 am, and between 4:00 and 6:00 pm, in order to make any needed adjustments. During these checks, the gas and waterflows, temperature, and oxygen concentrations were recorded. Oxygen concentrations near and below the air-saturation level were determined by the azide modification of the iodometric method (American Public Health Association, et al., 1965)*. Those above the air-saturation level were determined by the Pomeroy-Kirschman-Alsterberg modification.

Oxygen consumption rates of test fish were determined two days prior to the termination of some experiments with largemouth bass and coho salmon. Water samples for dissolved oxygen analyses were collected every two hours during the 24-hour oxygen consumption test period. Oxygen consumption rates of the fish were computed from differences of oxygen concentration in the inflow and outflow water sample bottles of each test vessel and expressed as milligrams oxygen consumed per gram dry weight of fish per hour (mg O_2/g-hr).

Results and Interpretation

Food consumption and growth rates were determined for juvenile largemouth bass, chinook salmon, and coho salmon held at various constant dissolved oxygen concentrations and temperatures and fed unrestricted rations of live food organisms. Appendix Tables 1, 3, and 5 list the total initial and final wet and dry weights, food consumption and growth rates and gross food conversion efficiencies for largemouth bass, chinook salmon, and coho salmon, respectively, and the dissolved oxygen concentrations and temperatures at which the fish were held. Appendix Tables 1, 3, and 5 also present the number of fish held in *each test chamber*, the date the experiment was initiated, and its length in days. The influence of dissolved concentration on the food consumption and growth of juvenile chinook salmon fed at low and moderately low levels on a cyclic basis (ration size being changed daily) was determined at 12 and 17C. The total initial and final wet and dry weights, food consumption and growth rates, and gross food conversion efficiencies for these salmon are presented in Appendix Table 4, along with the temperature, ration level, and dissolved oxygen concentration tested in each experiment. In the experiments reported herein, unless otherwise stated, growth rates are expressed in milligrams gained per gram mean weight of fish per day (mg/$\bar{g}$/day) and food consumption rates are expressed in milligrams food consumed per gram mean weight of fish per day (mg/$\bar{g}$/day).

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* American Public Health Association, American Water Works Association, and Federation of Sewage and Industrial Wastes Association. 1965. Standard methods for the examination of water, sewage, and industrial wastes. 12th ed. New York, 769p.

Largemouth Bass

Figure 2 presents the results of experiments conducted on the influence of reduced dissolved oxygen concentration on the growth rate of largemouth bass, held 17 to 30 days and fed to repletion on small live fish, at temperatures of about 10, 15, 20, 24, and 29C. At the temperatures of 29, 24, and 20C, dependence of growth rate of the largemouth bass on dissolved oxygen concentration at all oxygen levels below the air-saturation level was demonstrated. Similar relationships may be seen between food consumption rate and dissolved oxygen concentration at these moderate to high temperatures (Appendix Table 1). At 15C, dependence of growth rates on dissolved oxygen concentration was apparent only at levels below about 3.5 mg/l. Even less oxygen dependence was noted between growth rate of largemouth bass and dissolved oxygen concentration at 10C, the lowest temperature tested. Thus, a critical temperature above which growth rates of largemouth bass become markedly susceptible to depression by moderate reduction of the dissolved oxygen concentration appears to be between 15 and 20C.

An experiment was conducted on the influence of the number of fish held in a test chamber on the food consumption and growth rates of largemouth bass. One, five, and ten bass were placed in each of two test chambers and fed unrestricted rations of small live fish for 10 days at 20C. The initial and final weights, food consumption and growth rates, and gross food conversion efficiencies for these largemouth bass are presented in Appendix Table 2. The mean growth rates of one, five, and ten bass held in the 12-gal bottles and fed to excess were 29.9, 23.7, and 25.9 mg/$\bar{g}$/day, respectively. Thus, largemouth bass held individually in aquaria appear to grow somewhat better than those held at densities of five or ten fish per aquarium.

Chinook Salmon

The results of experiments on the influence of dissolved oxygen concentration on the growth of juvenile chinook salmon held for 20 days and fed

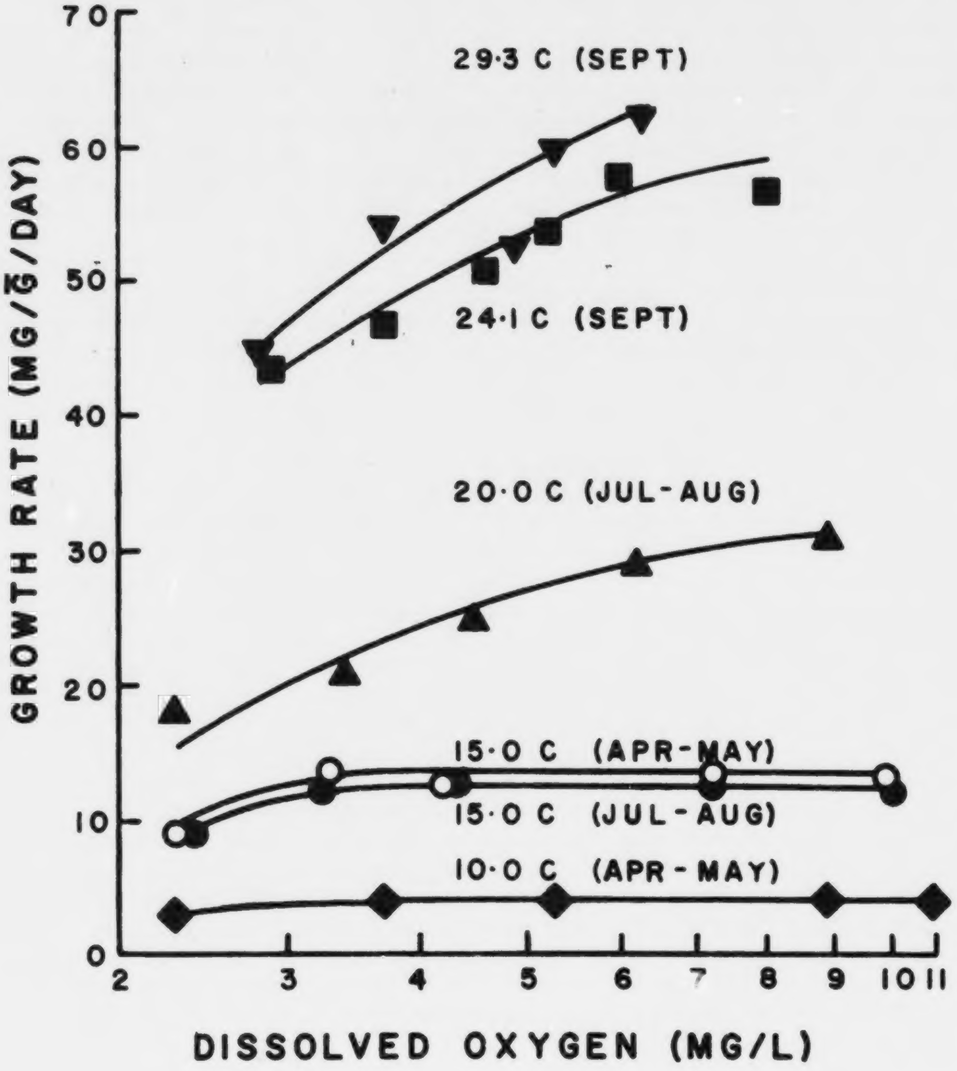

Figure 2. Relationships between mean dissolved oxygen concentration and growth rate of juvenile largemouth bass fed to repletion on small, live fish for 14 to 30 days at temperatures from 10 to 29C. Growth rates are based on dry weights.

unrestricted rations of tubificid worms at constant temperatures ranging from 8.4 to 21.7C are shown in Figure 3. In experiments conducted at temperatures of 21.7, 18.6, and 17.8C, the growth rate of chinook salmon appeared dependent on dissolved oxygen concentration at all levels below air saturation. Experiments conducted at 13.2, 13.0, and 8.4C showed little or no dependence of growth rate on dissolved oxygen concentration, until the concentration was depressed to levels below about 5 to 6 mg/l. The greatest independence of dissolved oxygen concentration occurred at 8.4C, the lowest tmperature tested. Chinook salmon reared at near air-saturation levels of dissolved oxygen grew more rapidly at 17.8C than did salmon reared at higher and lower temperatures. It is interesting to note that chinook salmon reared at 18.6C in July grew quite poorly in comparison to those reared at 17.8C a month earlier in June. A similar reduction in growth rate between experiments conducted in June and July was observed in studies with coho salmon, the results of which will be reported in the following section.

The influence of dissolved oxygen concentration on the food consumption and growth rates of juvenile chinook salmon fed tubificid worms on a weekly cycle of different daily rations varying from near starvation to excessive food was determined at 12 and 17C. The results of these experiments are presented in Figures 4 and 5 and in Appendix Table 4. As may be seen in these figures, the food consumption rate of chinook salmon fed low and moderately low cyclic rations tended to decrease with reductions in dissolved oxygen concentration at both temperatures tested. The growth rate of the salmon showed little or no decline with reduction in dissolved oxygen concentration below the air-saturation level. In fact, chinook salmon reared at the low cyclic rations at both temperatures in experiment 2 (Fig. 5) showed slight increases in their growth rates with decreasing dissolved oxygen concentration. This may in part be due to the fact that the salmon reared at the reduced dissolved oxygen levels were less active than those reared at air saturation, thus directing into growth energy and materials that would have been lost through activity.

In the experiments with cyclic rations (Appendix Table 4), the chinook salmon received food in excess on two consecutive days each week. On those days, food consumption was found to be dependent on dissolved oxygen concentration, with the greatest reduction occurring during the second day. Depression of the food consumption rate on the first day at reduced oxygen concentration was probably due to a direct effect on appetite. The somewhat greater depression of food consumption rate observed on the second day appeared to be due to an indirect effect on appetite through a direct reduction of the rate of food digestion.

Coho Salmon

Results of experiments conducted on the effect of reduced dissolved oxygen concentration of the food consumption and growth of juvenile coho salmon held for 13 to 20 days and fed unrestricted rations of tubificid worms at temperatures ranging from 8.6 to 21.6C are presented in

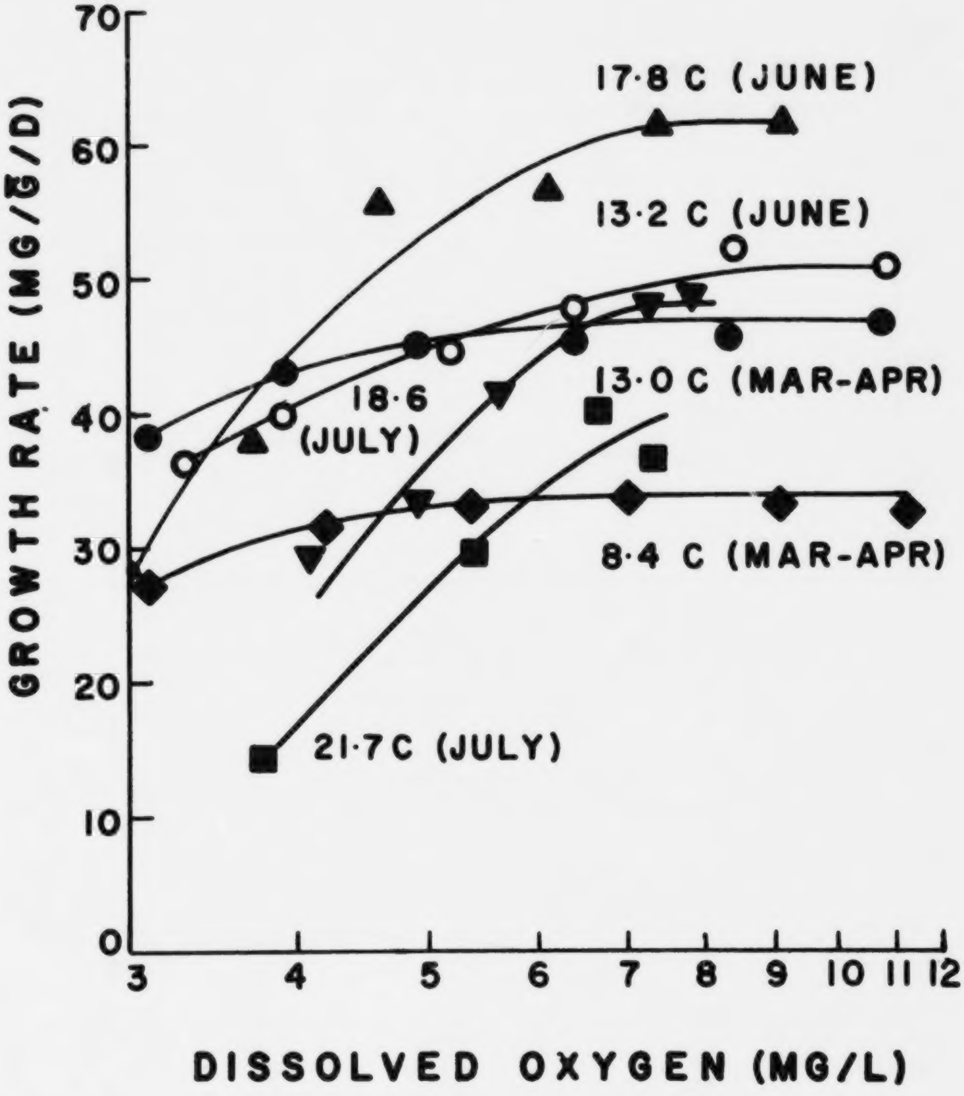

Figure 3. Relationships between dissolved oxygen concentration and growth rate of juvenile chinook salmon fed unrestricted rations of tubificid worms at temperatures from 8.4 to 21.7C. Growth rates of salmon are based on dry weights.

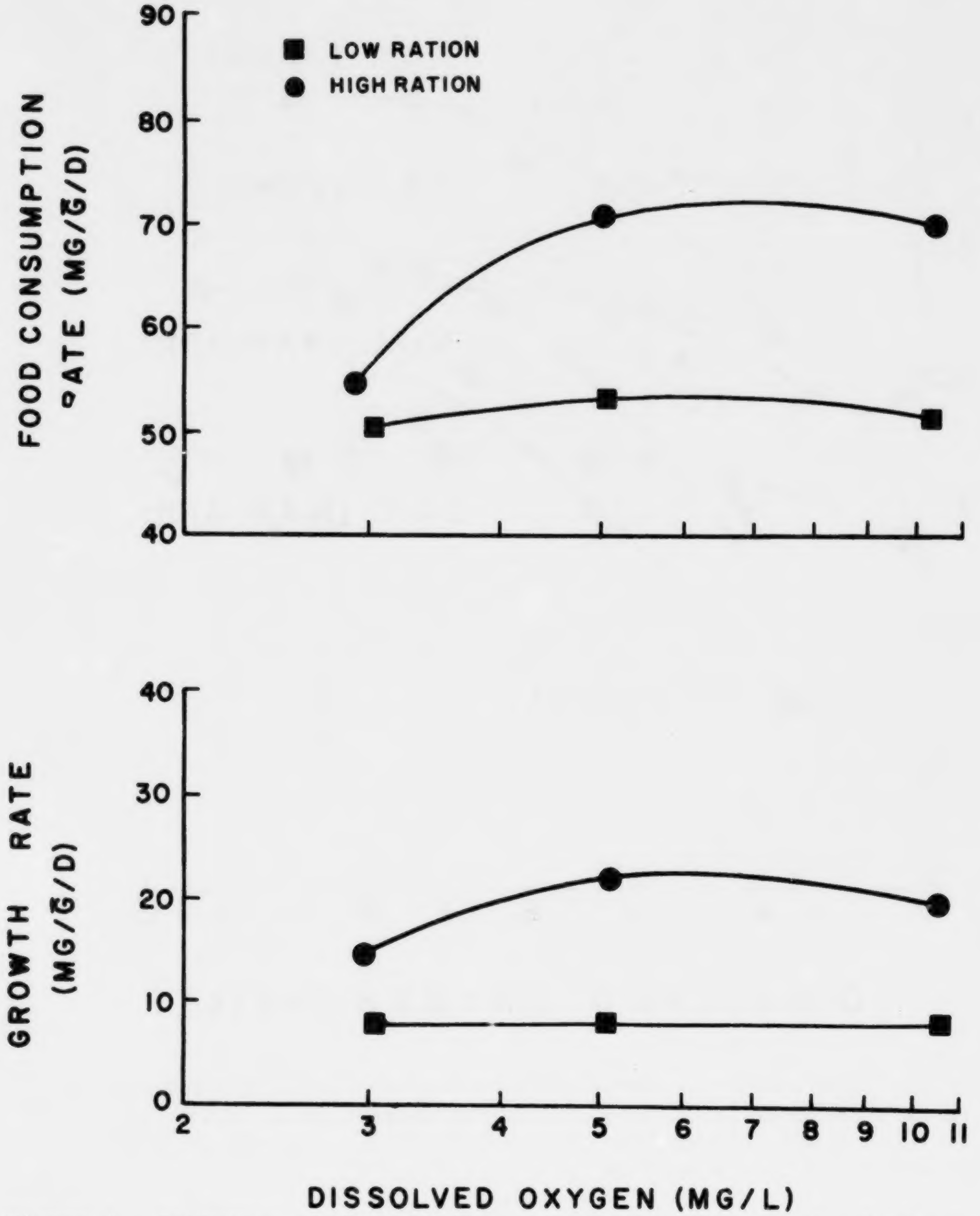

Figure 4. Influence of dissolved oxygen concentration on the food consumption and growth rate of juvenile chinook salmon held in aquaria at 12C and fed two fluctuating levels of ration of tubificid worms (see text for details of procedure). Growth rates of salmon are based on dry weights.

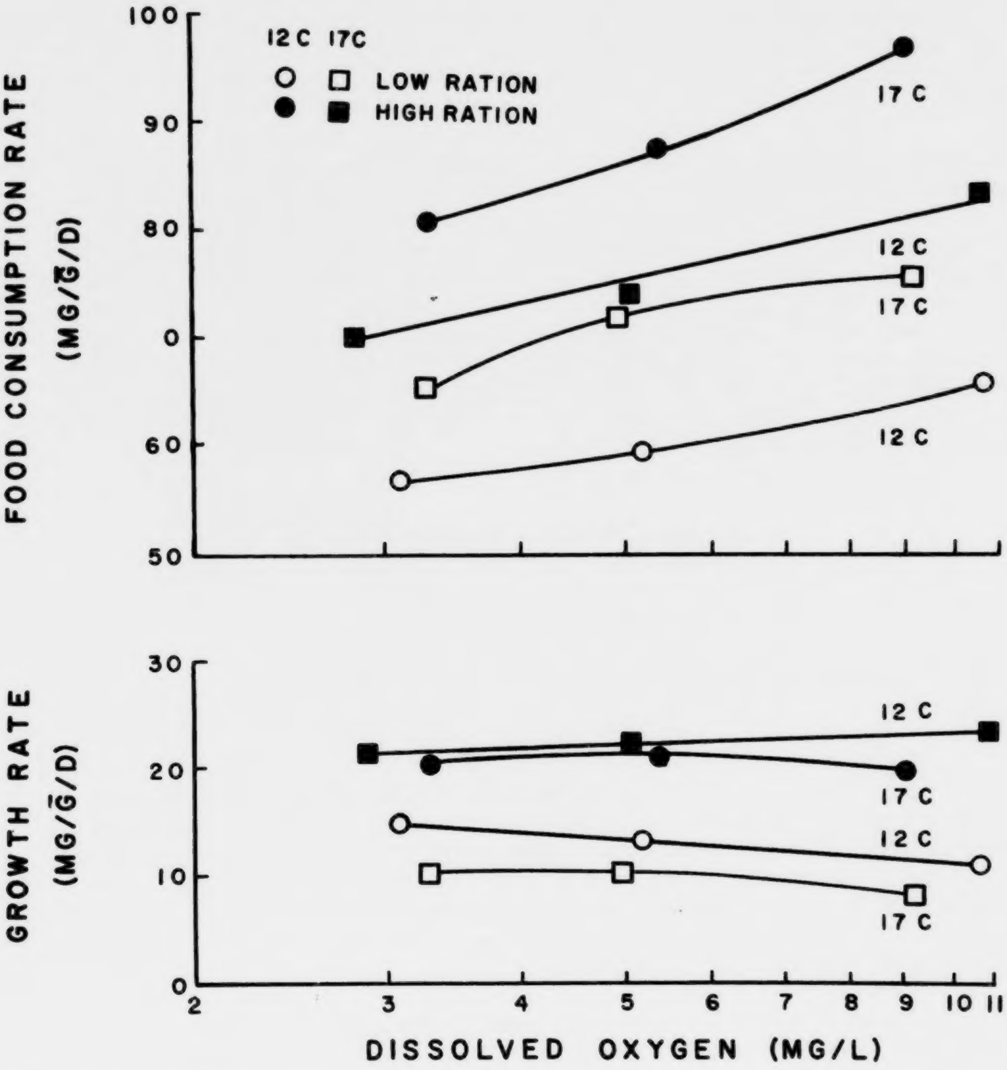

Figure 5. Relationships between mean dissolved oxygen concentration and food consumption and growth rates of juvenile chinook salmon held in aquaria at 12 and 17C and fed two fluctuating levels of ration of tubificid worms (see text for details of procedure). Growth rates are based on dry weights.

Figure 6 and Appendix Table 5. In general, the growth rate of coho salmon proved dependent on dissolved oxygen concentration at or only moderately below air-saturation levels at all temperatures tested. The growth rates of the salmon reared in May at 8.6C and in July at 18C, however, exhibited only minor depressions at dissolved oxygen concentrations as low as 5 to 6 mg/l. Chinook salmon reared at air-saturation levels of oxygen grew more rapidly in experiments conducted at temperatures near 18C than at other temperatures (Fig. 3); thus, higher and lower temperatures appeared to depress the growth rate of chinook salmon reared at air-saturation levels of dissolved oxygen.

As was noted above for chinook salmon, season of the year appears to play an important role in controlling the food consumption and growth rates of coho salmon. Coho salmon reared in June at 18.3C exhibited growth rates ranging from 52 to 65 mg/$\bar{g}$/day, coho salmon reared in July at 18C grew at rates near 23 to 34 mg/$\bar{g}$/day, and those reared in October at 18C grew at rates ranging from 10 to 37 mg/$\bar{g}$/day (Fig. 6). The same general relationship can be observed by comparing the growth rates of coho salmon reared at 12.9C in May with that of those reared at 13C in October. Similar differences in growth rates of coho salmon can be seen between those reared at near 21C in June and those reared at the same temperature in July.

RESPIRATION CHAMBER AND OTHER STUDIES OF BIOENERGETICS AND GROWTH OF COHO SALMON AS INFLUENCED BY DISSOLVED OXYGEN CONCENTRATION

Experimental Apparatus, Materials, and Procedures

Experimental Apparatus

Several types of test chambers were used in these experiments. A set of six respiration chambers, each with a cylindrical test compartment, was used in experiments on oxygen uptake rates, in which the fish were forced to swim continuously at nearly constant water velocities. The water velocity in each chamber could be varied from 0.3 to 0.7 feet per second by means of a small centrifugal pump. Figure 7 is a schematic drawing of one respiration chamber.

Six square aquaria made of styrofoam, each containing 12 liters of water, were used for these growth experiments. Each aquarium was subdivided with perforated plexiglas partitions into eight compartments. Each compartment contained about 1.5 liters of water. The water in each aquarium was renewed continuously, at a rate of about 200 ml/min. A manifold and plastic tubes distributed the water to the compartments of each aquarium. The styrofoam aquaria may be seen in the photograph presented in Figure 8.

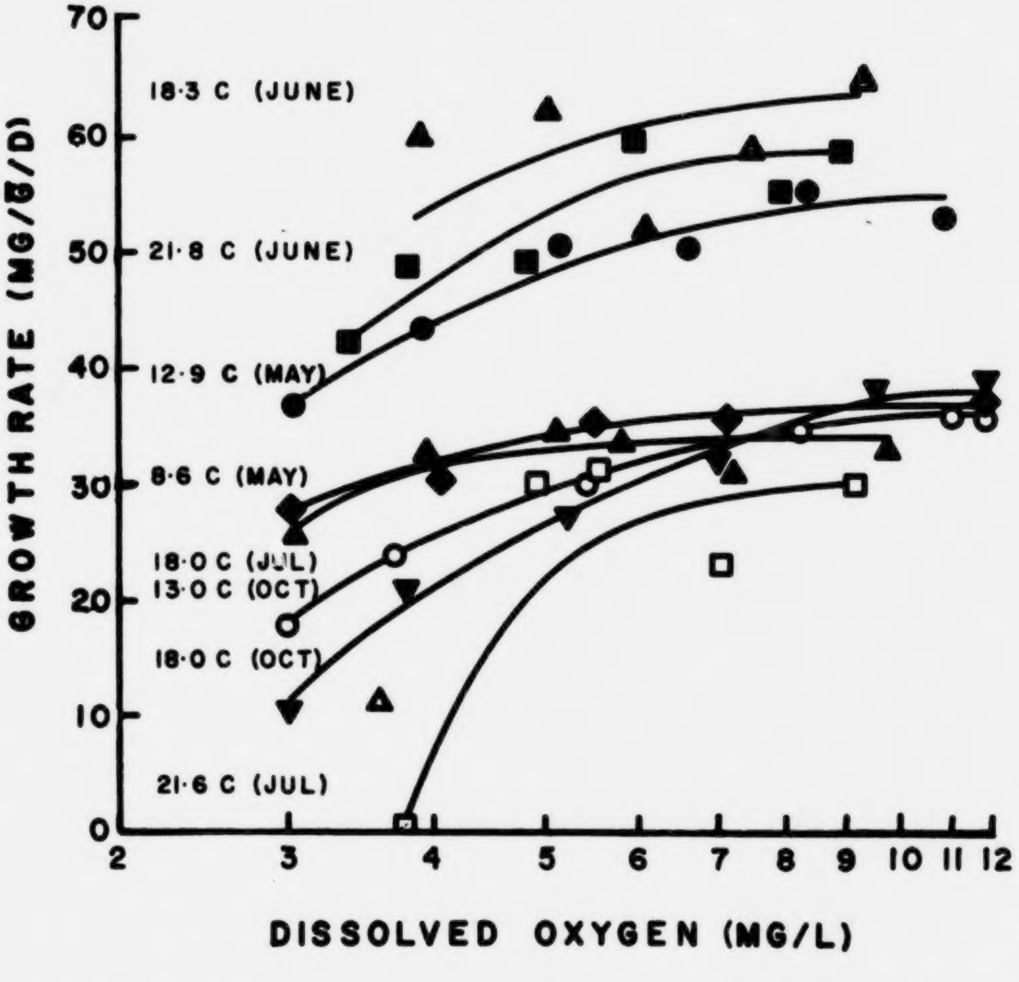

Figure 6. Relationships between dissolved oxygen concentration and growth rate of juvenile coho salmon fed unrestricted rations of tubificid worms at temperatures from 8.6 to 21.8C. Growth rates of salmon are based on dry weights.

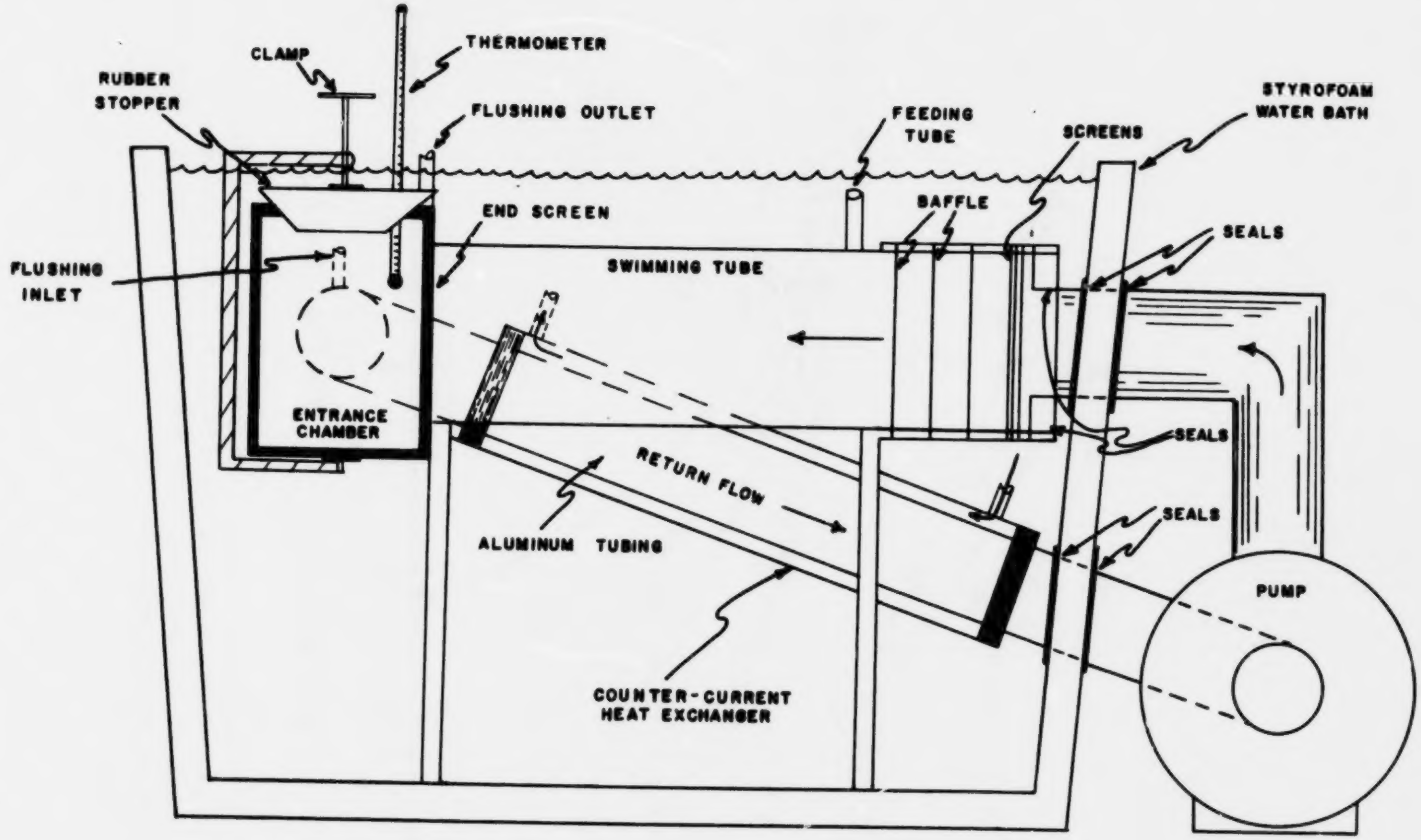
RUBBER STOPPER
CLAMP
THERMOMETER
FLUSHING OUTLET
FEEDING TUBE
SCREENS
STYROFOAM WATER BATH
FLUSHING INLET
END SCREEN
BAFFLE
SEALS
SWIMMING TUBE
ENTRANCE CHAMBER
SEALS
RETURN FLOW
SEALS
ALUMINUM TUBING
PUMP
COUNTER-CURRENT HEAT EXCHANGER

Figure 7. Schematic diagram of one of six respirometers used to determine oxygen consumption rates of coho salmon. The left side of the styrofoam water bath has been removed to show respirometer detail. Not shown is the variable speed device used to change pump speed.

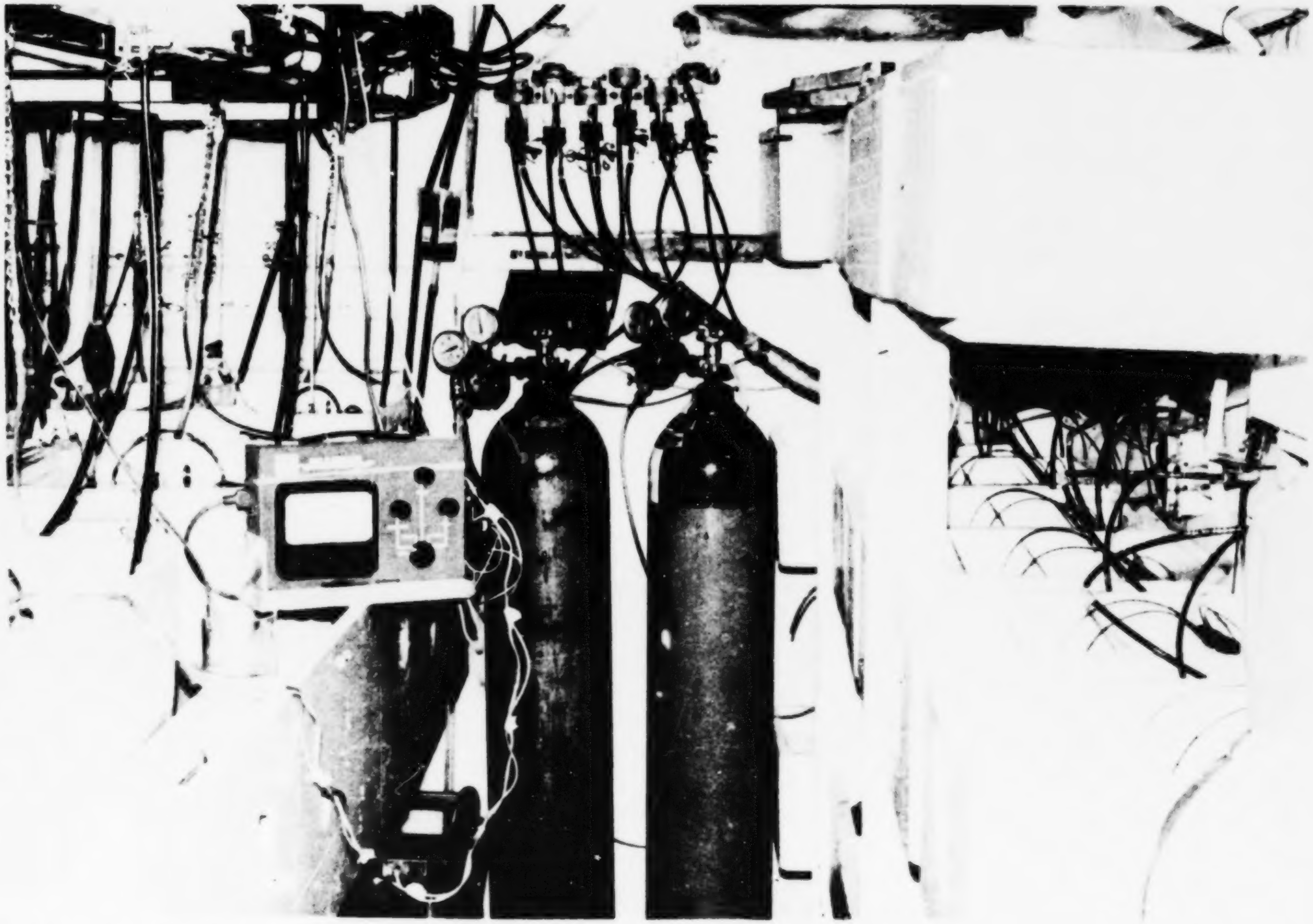

Figure 8. Photograph of some of the laboratory apparatus used in bioenergetic studies. The styrofoam boxes (water baths) at the left contained the respirometers. The styrofoam boxes shown at the right were used in the growth experiments.

Six, plexiglas chambers, each with two 1-liter compartments, were used for food assimilation efficiency studies. The water in these chambers was not circulated or renewed.

Dissolved oxygen concentrations of 8, 5, and 3 mg/l were maintained in each experiment. Two chambers or aquaria--each having eight compartments--were maintained at each concentration in the growth studies. In the oxygen uptake and growth experiments, the desired oxygen levels were maintained by passing the incoming water through glass columns having a counterflow of nitrogen. In the food assimilation efficiency tests, the dissolved oxygen concentration was controlled by continuously bubbling an air-nitrogen mixture through the water in each test chamber.

Experimental Material

The test fish used in these experiments were juvenile coho salmon collected periodically throughout the year from the Yaquina River near Nashville, Oregon. The size of salmon used in each experiment ranged from fry, recently emerged from the gravel, to fingerlings about one year old but not yet showing evidence of smolting. Once collected, the test fish were transported to the laboratory and placed in an aquarium and held at 15C for at least two weeks. During the two-week temperature adjustment period and during experiments, the salmon were fed live housefly larvae.

Experimental Procedures

After the two-week temperature adjustment period, the fish were held for at least nine days in the compartmented styrofoam aquaria (one fish per compartment). During this period, they were sparingly fed housefly larvae and were exposed daily for twelve hours to artificial illumination alternating with twelve hours of darkness. From the ninth to the fourteenth day of a 17-day period for acclimation to test conditions, the fish to be used in growth experiments were fed daily at the same rate they would receive during the growth tests. These salmon were then starved for two days, weighed and measured, and returned to the test chambers for an additional 24 hours before the tests proper were begun.

In preparation for the food assimilation tests, salmon were held individually in the compartmented styrofoam aquaria under test conditions and fed sparingly for a total of 14 days, and then they were deprived of food for two days, prior to initial weighing and transfer to the plexiglas test chambers.

Fish to be used in determination of standard metabolic rates and specific dynamic action of consumed food were transferred from the compartmented styrofoam aquaria to the respirometers after nine days of acclimation to the test conditions. In the respiration chambers, they were fed sparingly for five days and then deprived of food for two days before weighing and for one more day thereafter before the beginning of the experiments proper.

Four types of tests were performed with individual fish in the various types of experimental chambers. These included measurements of growth, food assimilation, standard metabolism and specific dynamic action of consumed food.

Growth. Each growth experiment consisted of 14 days of feeding in the compartmented styrofoam aquaria plus three days during which the fish were deprived of food before their reweighing at the end of the experiment. Daily records were kept of weights of food consumed by each fish and the experimental conditions of temperature and dissolved oxygen. Caloric values of samples of fish similar to those to be used in an experiment were initially determined. At the conclusion of an experiment, caloric determinations were made on all test fish. Caloric values of samples of the food fed were also determined.

Food assimilation efficiency. In these experiments, the fish were placed in the test chambers immediately after their initial weighing and were fed 24 hours later. After this they were held in the chambers for four days without food and their waste materials were allowed to accumulate. Each liter of water was then analyzed for ammonia nitrogen and chemical oxygen demand, and this data was converted to caloric value equivalents.

Standard metabolism. During these tests, the fish in the respiration chambers were deprived of food and were forced to swim for one-hour periods at each of several velocities between 0.3 and 0.7 ft/sec. Their oxygen consumption rates were measured during these periods, and after sufficient tests, the data were plotted on semilog graph paper, with swimming velocity and oxygen consumption rate as the coordinates. The oxygen consumption at zero velocity was then determined by extrapolation and taken to be the standard metabolic rate.

Specific dynamic action. These tests were performed in the respiration chambers used for the determination of standard metabolism. The baseline oxygen consumption rate of the fish was determined by making measurements every other hour during the two days of starvation that followed their five-day retention in the respirometer on restricted rations. They were then weighed and measured and returned to the respirometers for 24 hours. After this, the salmon were fed, and their oxygen consumption rate determined hourly until it returned to the base line. The total oxygen consumed over and above baseline consumption was attributed to specific dynamic action of the food (SDA).

Results and Interpretation

The data obtained from aquarium and respiration chamber experiments on the food consumption, growth, and bioenergetics of juvenile coho salmon are presented in Figures 9, 10, and 11, and in Appendix Table 6. The energy budgets shown in the figures were developed from all the data (after converting it to caloric values) obtained from the measurements of

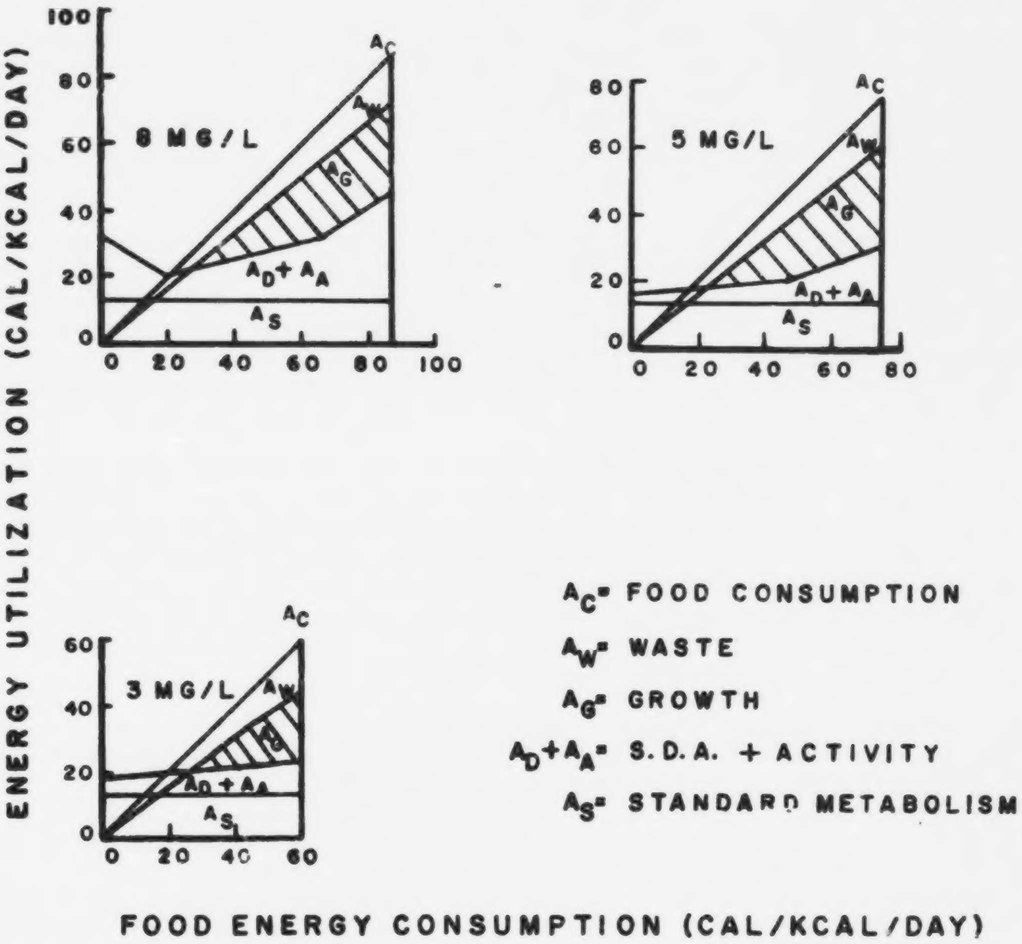

Figure 9. Relationships between food consumption rate, energy and material uses and losses, and dissolved oxygen concentration for juvenile coho salmon held at 15C during summer.

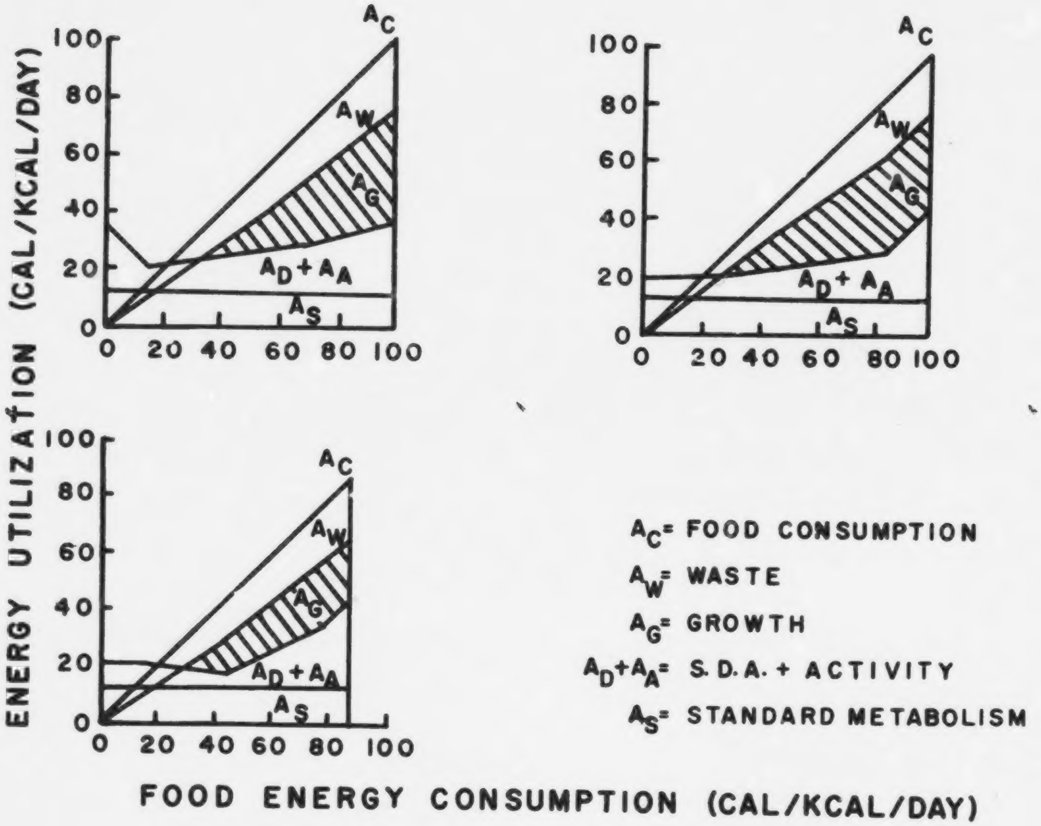

Figure 10. Relationships between food consumption rate, energy and material uses and losses, and dissolved oxygen concentration for juvenile coho salmon held at 15C during fall.

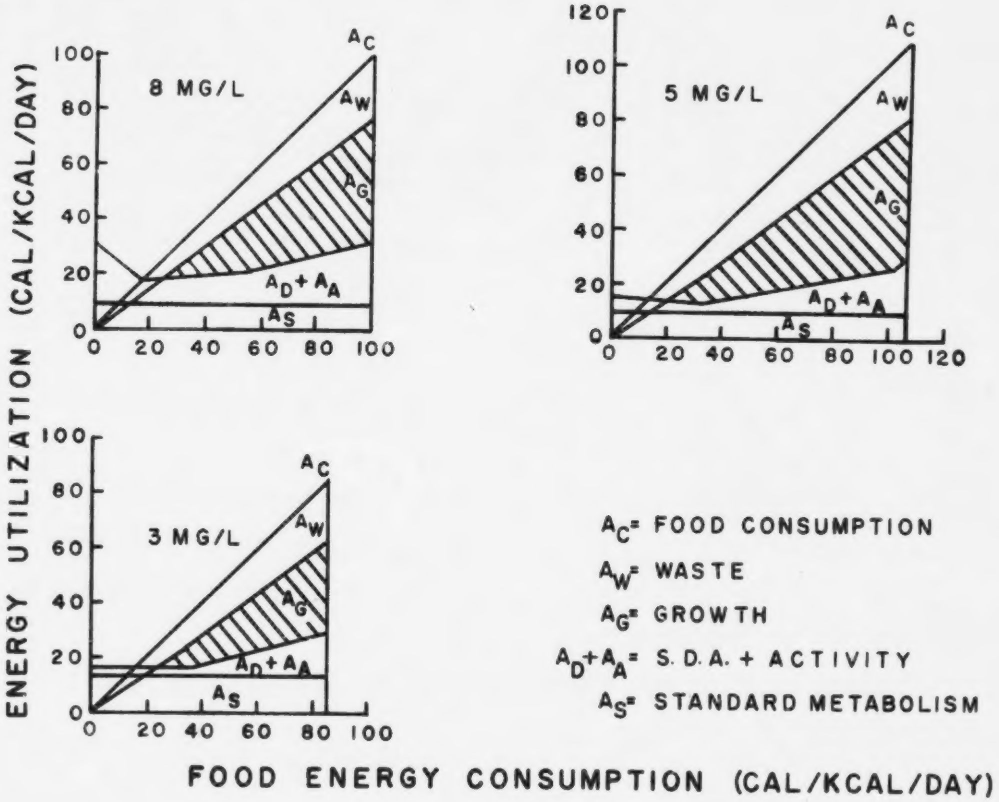

Figure 11. Relationships between food consumption rate, energy and material uses and losses, and dissolved oxygen concentration for juvenile coho salmon held at 15C during spring.

coho salmon food consumption rate, food assimilation efficiency, nitrogenous wastes, standard metabolic rate, and growth rate. Growth was measured at eight food consumption levels to obtain the growth information used in the budgets. Food assimilation efficiency and nitrogenous excretion were measured at three food consumption levels and standard metabolism was measured in recently starved fish in order to obtain data on waste products and standard metabolic rates for the budgets. The categories of muscular activity (A_a) and SDA (A_d) shown in the figures, were combined because of the difficulty of relating SDA determinations on swimming fish to actual levels in less active fish. This latter combined category was derived by subtracting the sum of total waste products, standard metabolism, and growth from the energy value of food consumed. Energy use illustrated in the budgets at zero food consumption came from utilization of previously formed tissues (i.e. loss in calories of body materials).

As is shown in the budgets for three seasons (Figs. 9, 10, and 11), the principal effect of reduced dissolved oxygen concentration was to restrict food consumption at 3 mg/l, the lowest test level. The fish at this low oxygen concentration in all cases exhibited much lower maximum food consumption rates than at 5 or 8 mg/l. Thus, the maximum possible growth rates of the coho salmon at 3 mg/l were much less than they were at the two higher levels of dissolved oxygen tested.

In the summer and spring seasons, the growth rates (indicated by the vertical heights of the shaded segment, A_g, at each food consumption rate) at 5 mg/l were greater than at the other oxygen concentrations over the entire food consumption range. In the fall, growth rates at 5 mg/l were higher than at the other concentrations at food consumption rates up to approximately 85 cal/kcal/day. Only in the fall at the highest feeding levels did the cohos at 8 mg/l show higher growth rates than those at 5 mg/l. At given consumption rates, the fish at 5 mg/l generally expended less energy for SDA and activity than those at 8 or 3 mg/l. This appears to be the principal reason for the generally better growth at 5 mg/l.

Another interesting observation concerning the expenditures for activity at zero food consumption is shown in Figures 9, 10, and 11. In all three seasons, unfed cohos tested at the oxygen concentration of 8 mg/l were much more active than those tested at 5 or 3 mg/l. Much of this excess activity was apparently due to "searching" for food. The starved fish at 8 mg/l often exhibited a frenzy of swimming for 20-30 minutes during the time nearby fish were being fed. Fish at other rations or dissolved oxygen concentrations often became quite active at feeding time, but this increased activity did not persist for more than four or five minutes.

Energy losses through wastes (A_w) and energy uses through standard metabolism (A_s) appeared to be largely independent of the dissolved oxygen concentration. Energy losses through fecal and nitrogenous waste products generally accounted for 20 to 30 percent of the energy value of the food consumed.

EXPERIMENTAL POND STUDIES OF THE BIOENERGETICS AND GROWTH OF LARGEMOUTH BASS AS INFLUENCED BY DISSOLVED OXYGEN CONCENTRATION

Experimental Apparatus, Materials, and Procedures

Experimental Apparatus

Two oval, concrete-lined, experimental ponds--approximately 6 meters in diameter and with a capacity of about 19,000 liters--were used in these experiments. A drawing of one of these ponds is shown in Figure 12. From a shallow peripheral area, the bottom of each pond slopes sharply to a central area, where the depth is about 1 meter. A rectangular observation chamber, with seven underwater glass ports, projects to near the center of each pond. Cylinders constructed of chickenwire and painted with non-toxic paint were placed end to end around the shallow periphery of the ponds to provide escape cover for the mosquitofish. These ponds are described in detail by Lee (1969).

Each pond was fitted with a transparent polyethelene cover sealed to the edge of the pond by a water seal and supported by a frame made of aluminum conduit (Fig. 13). These covers prevented the entry of unwanted food organisms and made it possible to maintain low-oxygen atmospheres above the ponds, this slowing reoxygenation of the pond water. Small wooden doors on both sides of the observation chambers slightly above the water level provided access to the ponds beneath the plastic covers.

Each pond was equipped with air lines supplying five dispersion stones, which were distributed evenly around the bottom of the pond and through which nitrogen or air could be forced. Introduction of oxygen or nitrogen through the stones promoted mixing of the water and helped to maintain the desired dissolved oxygen level.

The temperature of each pond was maintained by two 2000-watt, stainless-steel, immersion heaters controlled by thermoregulators. The water temperature was monitored with a continuously recording thermograph.

The well water in each pond was renewed continuously through a flowmeter at a rate of 4 to 10 liters/min. The flow rate was adjusted as necessary for maintaining the desired dissolved oxygen level and water temperature.

The water delivered to one of the ponds passed through a degasser, an apparatus designed by Mount (1964)* to remove dissolved gases from water.

Mount, D. I. 1964. Additional information on a system for controlling the dissolved oxygen content of water. Trans. Amer. Fish. Soc. 93:100-103.

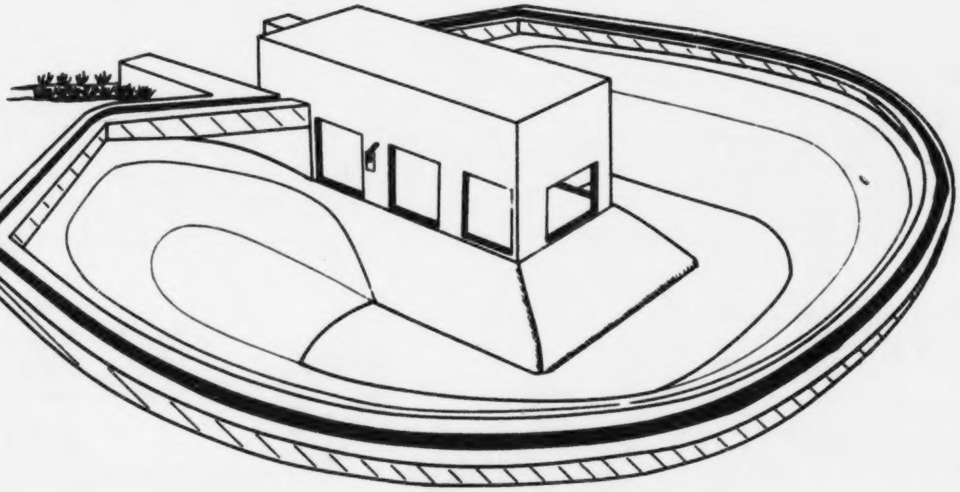

Figure 12. Schematic drawing of one of two experimental ponds used in this study. Each pond was equipped with an observation chamber, temperature control equipment, and an adjustable standpipe to maintain the desired water level in the pond.

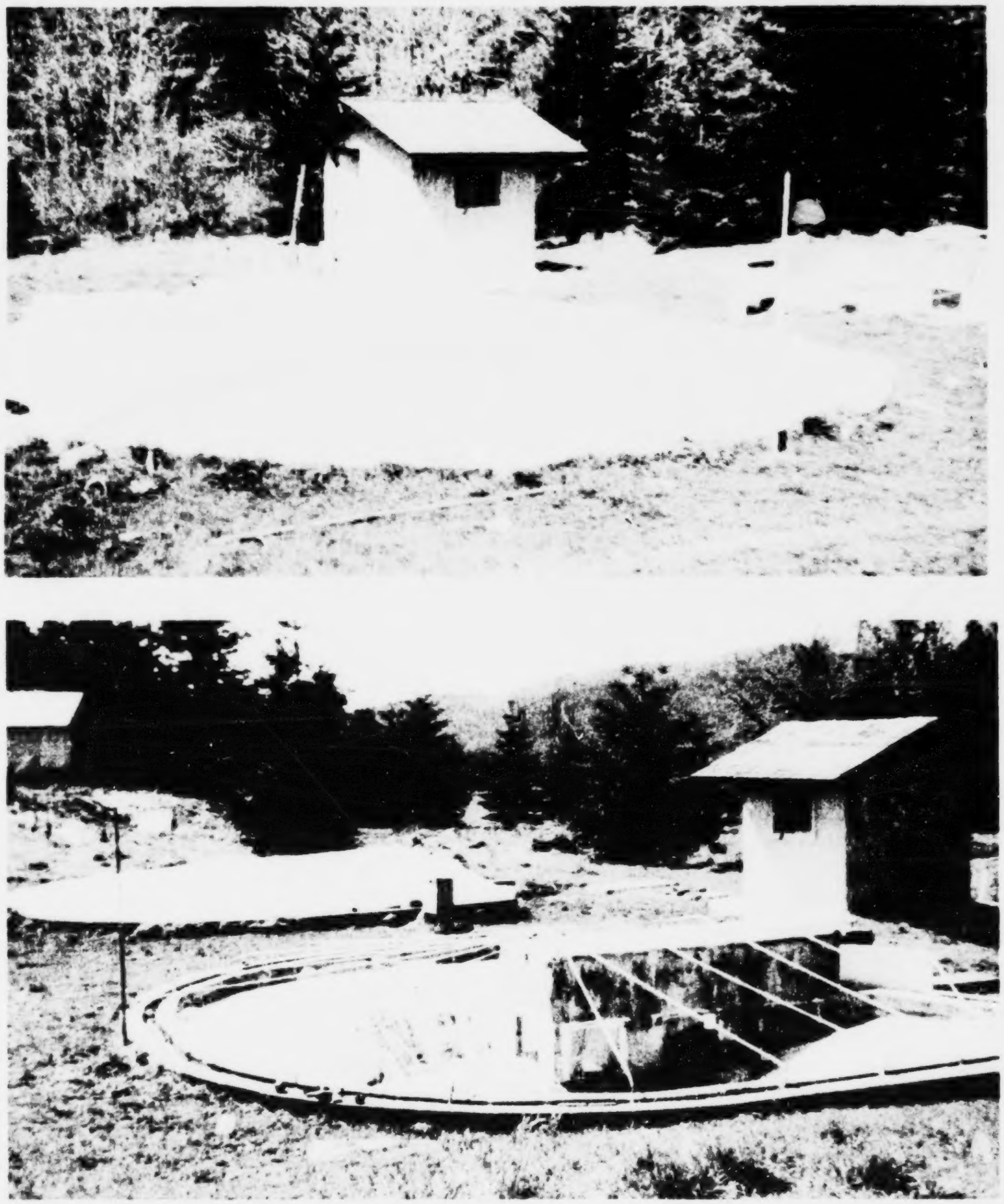

Figure 13. The experimental ponds shown with and without the plastic cover. The degasser and other associated equipment were housed in the small building.

Once in the degasser, water is circulated by a pump through a vacuum chamber where the gases come out of solution and are removed continuously with a vacuum pump. A mixture of renewal and recycled pond water passed through the degasser at a rate of 15 to 25 l/min. The water flow through the degasser and the vacuum were adjusted to produce the desired dissolved oxygen concentration in the experimental pond.

Experimental Materials

The largemouth bass used in these experiments were seined from a pond near Jefferson, Oregon. The fish were graded according to size and only those up to 120 mm in length were selected. The bass were transported to the Oak Creek Laboratory and were placed in 190-liter glass aquaria held near 18C. During this holding period, the bass were fed live mosquitofish.

The mosquitofish used as food for the bass were collected from several small log ponds in the local area. It was necessary to collect mosquitofish from more than one source because of limited abundance and because the fish in some areas became diseased as the water fell to a low level in the late summer. After transportation to the laboratory, the mosquitofish were held outdoors in a wooden tank equipped with a 2000 watt stainless-steel immersion heater and were fed Oregon Moist Pellet.

Experimental Procedures

These experiments were 14-day tests during which bass were maintained in both experimental ponds simultaneously on equal densities of mosquitofish. During each experiment, the dissolved oxygen concentration of the water in one pond was maintained at the air-saturation level, while that of the other was reduced to a desired level. An attempt was made to avoid any other differences in test conditions, such as temperature, water level, exchange rate, during an experiment. Several days before the start of an experiment, the ponds were filled with water and regulated to the desired test conditions.

Once the test conditions had been established in each pond, an appropriate number of mosquitofish of fairly uniform size was selected from the available stock. The largest and smallest individuals and those that appeared unhealthy or were in late stages of pregnancy were not used. After an adequate quantity of mosquitofish had been selected, one of two techniques was used to select samples of the mosquitofish before each experiment. In experiments 1, 2, 3, and 7, samples of about 5 grams of mosquitofish were sacrificed, dried to a constant weight in an oven at 70C, and then reweighed to obtain dry weights. In the remainder of the experiments, samples consisting of 50 mosquitofish were selected at random and handled in the manner described above.

The desired weight of mosquitofish was stocked in the ponds two days before the beginning of each experiment to allow these prey animals to become oriented before the bass were introduced. Normally, 170 g of mosquitofish were placed in each pond, but in experiments 6 and 7 the initial prey densities were 100 and 240 g per pond, respectively. The quantity of mosquitofish in the ponds decreased as they were consumed by the bass. No attempt was made to replace the prey fish eaten during the test period, because it was observed that mosquitofish recently placed in the pond were initially disoriented and easily captured by the bass, thus upsetting the more natural prey-predator relationship previously established. The prey density was thus permitted to decrease during the experiment, sometimes to about one-half of the initial level.

Since the experimental ponds contained little or no food for the mosquitofish, a small quantity of a dry commercial guppy food was fed at a rate estimated to be a maintenance ration--the ration that would allow neither weight gain nor loss during the experimental period.

Several days before the start of each experiment, 10 bass of similar size were selected from the available stock, individually marked with the cold-brand technique described by Ellis (1968),* and then returned to a 190-liter aquarium and held at the temperature to be maintained in the ponds in the ensuing experiment. At the start of the experiment, the marked bass were individually weighed and measured, and four bass were placed into each experimental pond. The bass were selected to provide about the same total weight in each pond. The two remaining bass were sacrificed and dried to a constant weight in an oven at about 70C.

During the experiments, experimental conditions were checked twice daily; and, when necessary, adjustments were made in the temperature, dissolved oxygen concentration, and water level in the ponds. The dissolved oxygen concentration in each pond was determined at least twice daily using the azide modification of the iodometric method (American Public Health Association, et al., (1965)**. Adjustments of the dissolved oxygen concentration in the pond were made by changing the amount of nitrogen being dispersed through the water, by adjusting the amount of vacuum in the degasser, or by changing the amount of water circulating through the degasser.

When each experiment was terminated, the bass and remaining mosquitofish were removed from the ponds. The bass were identified according to their marks, individually weighed, measured, sacrificed, and dried to a constant weight. The mosquitofish were weighed in aggregate and samples were taken and processed in the manner described above.

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* Previously cited.

** Previously cited.

In every experiment both planktonic and filamentous algae grew much faster in the pond held at the reduced oxygen level than in the pond held at the air-saturation level. Although the exact cause of the difference in the growth rates of algae in the two ponds is not known, it may have been due to the difference in oxygen concentrations. Gibbs (1970)* reported that in many kinds of plants, including algae, the production of usable photosynthate is measurably reduced in the presence of normal oxygen concentrations. Growth reportedly increased as the level of oxygen in the plant's environment decreased.

The oxygen produced by the algae during photosynthesis caused large diurnal fluctuations in the dissolved oxygen concentration of the water in the pond which made it difficult to maintain a reduced oxygen level. The algae may also have influenced food availability by reducing the visibility more in the pond with the heaviest algal growth. To control the algal growth, both ponds were treated with an 80 percent preparation of simizine (2-chloro-4, 6, bis [ethylamino]-s-triazine) at a concentration of 3 mg/l. The ponds were treated with simizine during each of the experiments, except experiment 1. Normally, the excessive algae growth was effectively controlled by one treatment near the beginning of each experiment, but two treatments were required for experiments conducted during the late summer months.

Results and Interpretation

Results of this investigation show that the food consumption and growth rates of juvenile largemouth bass reared in experimental ponds, at moderate densities of prey fish, increased with temperature and decreased with moderate reductions of dissolved oxygen concentration below the air-saturation level, except at low temperatures. Appendix Table 7 lists the individual initial and final weights and lengths and the growth rates of largemouth bass held for two weeks in the experimental ponds. The mean temperatures and dissolved oxygen concentration and initial prey densities for each experiment are also given in Appendix Table 7. The initial and final prey densities, food consumption rates of the bass, and the wet and dry weights and caloric content of the initial and final samples of mosquitofish used in each experiment are presented in Appendix Table 8. The growth of bass during the experiments was determined by direct measurement; food consumption was estimated from the change in mosquitofish biomass during the experiment.

The weight gained by bass held in the experimental ponds was determined by calculating the difference in the initial and final weights of each bass. The growth values were converted to rate terms to provide a

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Gibbs, M. 1970. The inhibition of photosynthesis by oxygen. Amer. Sci. 58:634-640.

basis for comparison between experiments. Growth rates are expressed in terms of milligrams of weight gained per gram of mean weight of bass per day (mg/ḡ/day). These were calculated by dividing the amount of wet weight gained during the test period by the mean weight (i.e., the average of the initial and final wet weights) of the individual bass. The gain in weight per mean gram of bass was then divided by the length of the experiment in days. The growth rates of the individual bass were averaged to provide mean growth rates for each experiment. The food consumption rates are also expressed in milligrams per mean gram of bass per day (mg/ḡ/day). These were calculated by dividing the total wet weight of mosquitofish consumed by the average total weight of bass in the pond during the test period, and finally by the number of days in the test period.

Figure 14 shows the relationships between the growth rates of largemouth bass held at high and moderately reduced oxygen concentrations at an initial prey density of 170 g/pond and at temperatures ranging from 13.3 to 27.6C. The upper curve was fitted to the growth rates of individual bass held in the experimental ponds at oxygen concentrations near the air-saturation level. The lower curve was fitted to the growth rates of individual bass held at oxygen levels 4 to 6 mg/l *below* air-saturation levels, with the exception of the high values plotted at 26.5C. The high values at 26.5C were not used in fitting the curve, because the dissolved oxygen concentration of the pond during this test was only about 2.5 mg/l below the air-saturation level. Both curves were visually fitted.

As can be seen from the upper curve in Figure 14, the mean growth rates of the bass reared near air-saturation oxygen levels increased from 11.4 mg/ḡ/day at 13C to 38 mg/ḡ/day at 27C. At the reduced oxygen levels, a similar increase in temperature resulted in an increase in mean growth rates from 11.4 mg/ḡ/day at 13C to 27 mg/ḡ/day at 27C. The distance between the two curves illustrates the amount growth was depressed at each test temperature by a 4 to 6 mg/l reduction in dissolved oxygen concentration. The greatest reductions in growth rate caused by reduced oxygen concentration occurred at the higher temperatures, at which the fish grew more rapidly. The vertical distance between the points plotted at each test temperature shows that the variation between growth rates of individual bass was also greater at temperatures at which the bass grew more rapidly.

In experiments 5, 6, and 7, largemouth bass were provided initial prey densities of 170, 100, and 240 g per pond, respectively. During the experiments the ponds were maintained at about 18C, and dissolved oxygen concentrations near air saturation in one pond and 4.7 mg/l in the other (Appendix Table 7). Bass in the experiments having the higher initial mosquitofish density of 240 g per pond grew substantially more than those in experiments having either of the lower prey densities. The food consumption and growth rates of bass held at reduced dissolved oxygen levels were restricted at all three prey densities tested, but the percent reduction in growth rate was greater at higher prey densities.

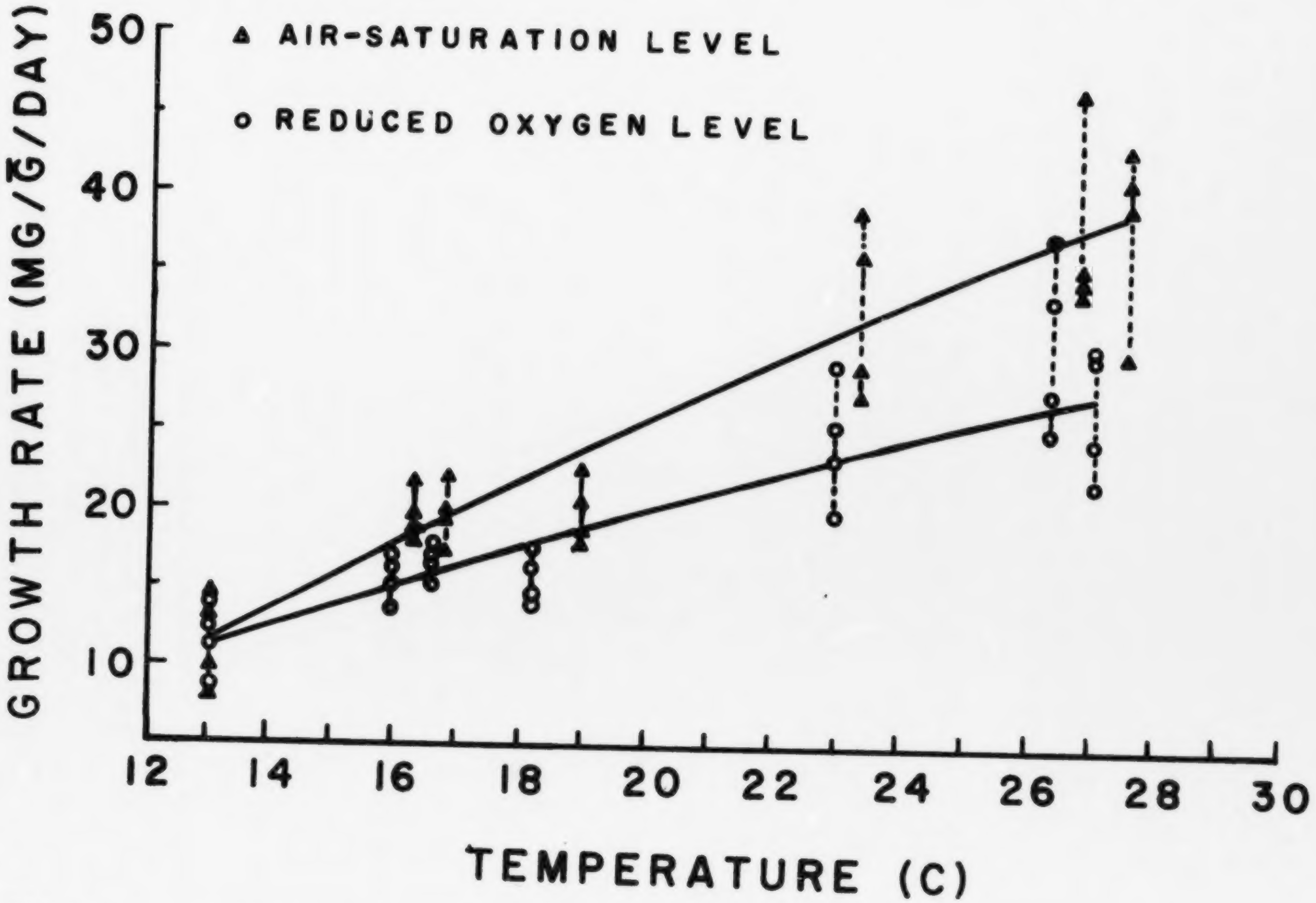


Figure 14. Relationships between water temperature and growth rate of individual largemouth bass reared in the experimental ponds at near air-saturation and reduced (4 to 6 mg/l below air-saturation) dissolved oxygen levels. The ponds were stocked with an initial mosquitofish biomass of 170 g/pond.

As the mosquitofish were preyed upon by the bass during the experiments, the total weight (density) of the mosquitofish in each pond was gradually reduced (Appendix Table 8). Since prey fish were not added during the course of the experiments, the prey densities normally fell to about 40 to 60 percent of the initial level by the end of an experiment. At the low prey density of 100 g per pond, however, the bass in experiment 6 consumed 74 percent of the mosquitofish initially added. Because of the lower food consumption rates of bass held at the reduced dissolved oxygen level in each experiment, the greatest variation in prey fish density occurred in the pond held at air-saturation level, except at low temperatures. This probably reduced the apparent effect of reduced dissolved oxygen concentration on growth, since food was relatively more abundant in the low-oxygen ponds toward the end of experiments even though the prey biomass was the same in both ponds at the beginning of each experiment.

The wet and dry weights and caloric values of the mosquitofish samples collected before and after each experiment are presented in Appendix Table 8. An estimate of change in the condition of the mosquitofish can be made by comparing the ratio of dry to wet weights or the caloric values of the initial samples to those of the final samples. The data in Appendix Table 8 show that there was little or no change in the condition of the mosquitofish during the experiments, except in experiment 2. In this experiment, the mosquitofish appear to have utilized bodily energy reserves, probably because they were fed insufficient food during the course of the experiment.

The results of statistical tests of differences in the mean growth rates of the bass reared at high and reduced dissolved oxygen levels in each experiment are presented in Appendix Table 9. At the 95 percent confidence level, the "t-test" values computed for differences in the mean growth rates show a significant difference for all experiments except 1, 2, and 10. Experiments 1 and 2 were conducted at a relatively low temperature (near 13C) and the difference in the dissolved oxygen concentrations tested had essentially no effect on the growth or food consumption of the bass. Experiment 10 was maintained at 26C, a relatively high temperature, resulting in a large variation in individual growth rate values, but the small reduction in dissolved oxygen concentration (8.3 mg/l to 5.8 mg/l) caused only a small difference in growth rates between the two ponds. The variance within all the samples increased with temperature and was usually greater at the higher oxygen level in each experiment.

Figure 15 illustrates the relationship between the mean growth rates and food consumption rates of largemouth bass held in the ponds for two-week test periods. The growth and food consumption rates plotted in Figure 15 are also given in Appendix Tables 8 and 9. Values are not included for experiment 2, because the individual mosquitofish appear to have lost substantial weight during that test period. Although several different variables are involved (oxygen concentration, temperature, prey density, season), the coefficient of linear correlation between the mean growth and food consumption rates of bass reared in the ponds

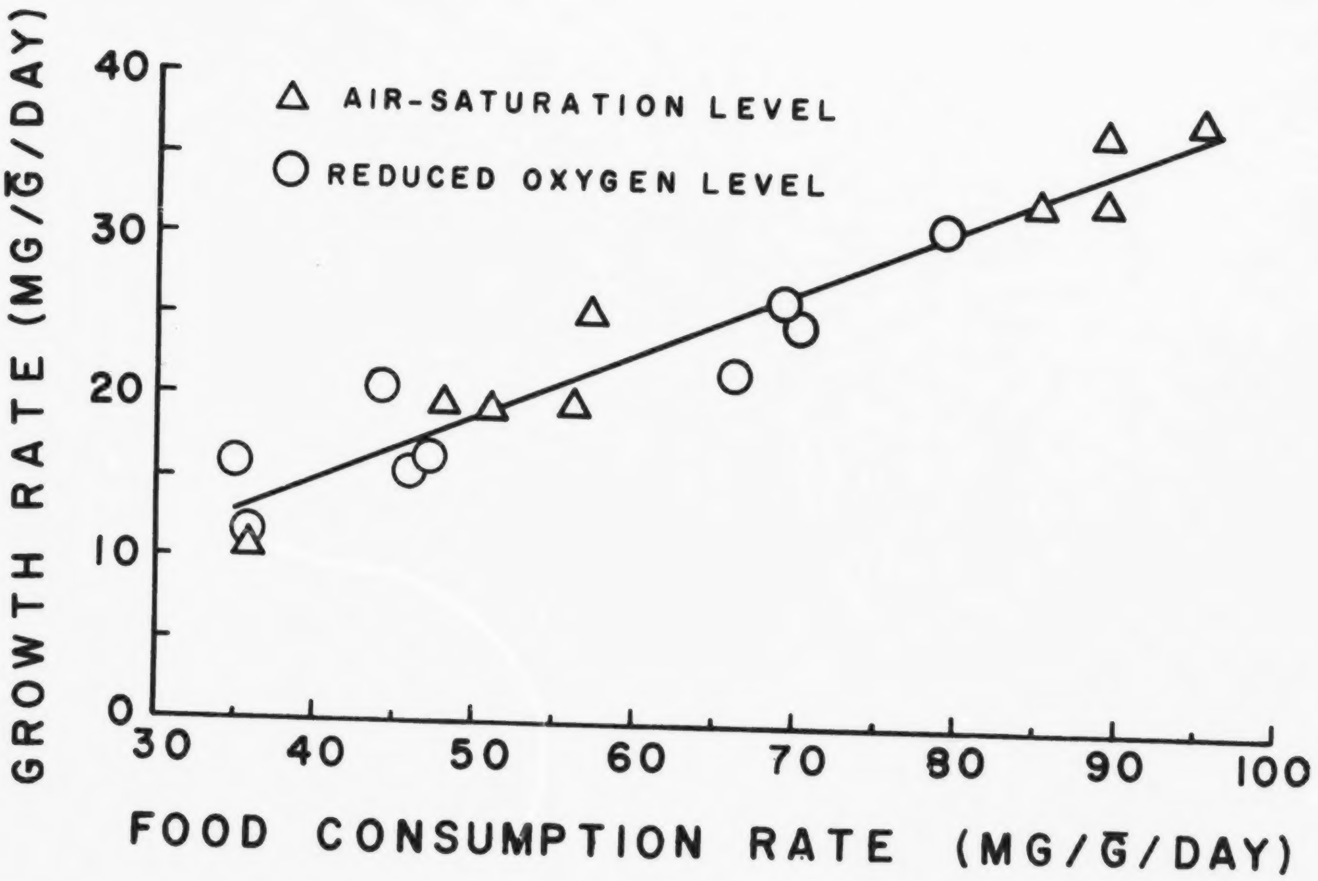


Figure 15. The relationship between mean growth rate and rate of food consumption of largemouth bass reared under various conditions of dissolved oxygen, food density, and temperature, in the experimental ponds.

was 0.96. This strong relationship suggests that regardless of the factors controlling food consumption, the proportion of the consumed food materials required for metabolic processes remained the same with increasing consumption rates.

LABORATORY STREAM STUDIES OF THE GROWTH OF CHINOOK SALMON AS INFLUENCED BY FOOD DENSITY AND DISSOLVED OXYGEN CONCENTRATION

Experimental Apparatus, Materials, and Procedures

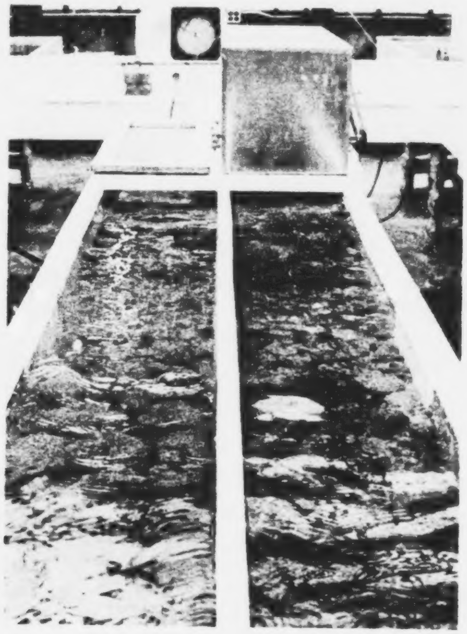
Experimental Apparatus

Nine laboratory streams were used in this investigation (Fig. 16). Each stream consisted of two wooden troughs (each 12" by 12" by 120") placed side by side with openings in the adjacent sides near both ends of the troughs permitting circulation of water, down one trough and back the other. Stainless steel paddle wheels were used to maintain this circulation providing a stream current velocity of about 0.5 ft/sec. In order to seal each stream from the atmosphere, a metal cover was placed over the paddle wheel and a transparent plastic cover was fitted over the remainder of the stream. The photographs presented in Figure 16 show one laboratory stream with its cover removed and other streams with covers in place. The bottoms of the streams were covered with near-equal amounts and assortments of natural stream rubble and gravel. This material was arranged in each stream in a manner to form four riffles and six pools. The water in each stream was exchanged with sand-filtered stream water at a rate of 1.5 liters/min.

The laboratory streams were housed in a building with a translucent plastic roof allowing sunlight to enter. During the summer months of June, July, and August, temperatures and light levels in the building were controlled to a limited degree. To reduce the light level, a greenhouse compound was applied to the plastic roof of the building, and burlap strips were placed directly on the plastic, stream covers. The greenhouse compound also served to reduce the air temperature in the building. Further control of the air temperature was provided by drawing large quantities of air into the building through large fiber mats that were kept wet. No direct attempt was made to control water temperature in the streams.

Experimental Material

Juvenile chinook salmon were periodically obtained by seining from the Sixes River and its tributaries on the southern coast of Oregon. Once collected and transported to the laboratory, the young salmon were held in laboratory streams similar in construction to those described above. During the time the stock of fish was maintained in these streams, they were fed daily a near-maintenance ration of live tubificid worms and



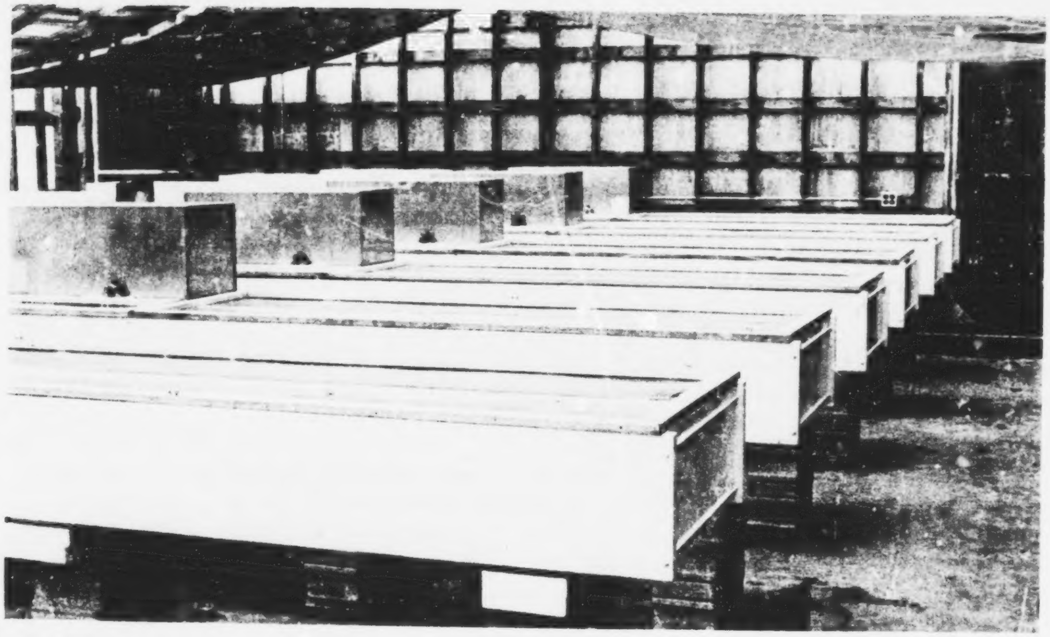


Figure 16. Photographs of some of the nine laboratory streams used in this investigation. The translucent plastic and metal paddlewheel covers are in place in the lower photograph. Shading material is shown draped over the streams.

Oregon Moist Pellet. During experiments, however, the fish in the laboratory streams subsisted on food organisms, mainly insect larvae, produced in the streams.

Experimental Procedures

Prior to the start of an experiment, the streams were colonized rather uniformly with algae and insects collected from two small streams in the local area. After the colonization, time was allowed for the organisms to become well established. Once the streams were colonized, a bottom (benthic) sample consisting of 0.5 ft^2 of pool bottom and 0.5 ft^2 of riffle bottom was removed from each stream and analyzed for fish-food organisms.

At the start of an experiment, juvenile chinook salmon were selected from the available stock of fish. The salmon were individually weighed and measured and were marked by the cold-brand technique. The marked fish were allowed a few days to recover from this handling before they were introduced into the laboratory streams. Equal numbers and nearly equal total weights (biomasses) of salmon were placed in each stream. The number of salmon placed in each stream varied from 2 to 4 in different experiments, according to the size of the fish and food level in the streams. At the time the salmon were placed in the streams, an initial sample of salmon, similar in size and condition to those introduced, was removed from the stock stream and the ratio of wet weight to dry weight determined.

Immediately after the salmon were introduced, the stream covers were put in place and sealed. Flows of nitrogen gas and air were then introduced under the covers of the streams, in order to adjust the dissolved oxygen content of the water to the desired levels. About 12 hours were required to reduce the dissolved oxygen concentration to near 3 mg/l, the lowest level tested. During the 20 and 27-day experiments, drifting food organisms were collected continuously by passing the water discharged from the streams through a fine-mesh plankton net. In the 10-day experiments, drift samples were collected continuously for eight of the ten days. During the course of an experiment, dissolved oxygen concentrations and gas and water flow rates were determined daily and adjusted as necessary. Temperatures were continuously recorded.

At the termination of each experiment, the chinook salmon were removed from the streams and placed in 5-gallon containers, where they were kept for 24-hours, to allow for the digestion of stomach contents. The salmon were then sacrificed, and wet and dry weights were determined. Once the salmon were removed from the streams, bottom samples like those described above were taken from each stream and analyzed for fish-food organisms.

Results and Interpretation

The influence of reduced dissolved oxygen concentration on the growth of juvenile chinook salmon held in laboratory streams was studied in nine experiments, which varied in length from 10 to 27 days. Appendix Table 10 gives the initial and final wet and dry weights and the growth rates of the chinook salmon, the mean dissolved oxygen concentrations, and average stream temperatures. Also presented in Appendix Table 10 are the number and biomass of salmon placed in each stream, the starting date and duration of each experiment, and the densities of food organisms present in the benthos and drifting in the current.

In experiments 1, 3, 4, and 8, conducted at average temperatures of 9.0, 11.6, 13.5, and 14.3C, respectively, the growth rates of the chinook salmon were found to be dependent on the dissolved oxygen concentration. In these experiments, the average biomasses of salmon introduced into the streams were relatively low, ranging from 1.1 to 2.2 g/m^2. This tended to make the relative abundance of food per unit of fish biomass rather high. Figure 17 presents the results of experiments 3 and 4, which show dependence of growth rate on dissolved oxygen concentration. In general, the data presented in Figure 17 and Appendix Table 10 suggest that the higher temperatures tested, when coupled with high food availability, led to greater dependence of growth rate of the salmon on dissolved oxygen concentrations. As can be seen in Figure 17, the growth rates of salmon held at 13.5C showed a fairly strong dependence on dissolved oxygen concentration at all levels tested, while the growth rates of salmon held at 11.6C showed dependence only at oxygen concentrations of about 5 mg/l and below.

In experiments 2, 5, 6, 7, and 9, growth rates of the chinook salmon were found to be independent of dissolved oxygen concentration. The results of two such experiments (experiments 2 and 8) are presented in Figure 18. The salmon biomasses in the experiments showing oxygen independence ranged from 2.2 to 4.9 g/m^2--consistently higher than the salmon biomasses in experiments showing oxygen dependence (1.1 to 2.2 g/m^2). Thus food was relatively less available to the salmon in the experiments showing independence of growth rate on oxygen concentration (Appendix Table 10). Lower food availability appears, then, to have led to lower food consumption and the substantially lower growth rates of salmon in experiments showing no dependence as compared with the growth rates of salmon in experiments showing dependence on dissolved oxygen concentration (Appendix Table 10). At near air-saturation levels of dissolved oxygen, coho salmon in experiments 3 and 4 (Fig. 17) grew at rates from about 35 to 60 mg/$\bar{g}$/day, while the growth rates of salmon at similar dissolved oxygen levels in experiments 2 and 7 (Fig. 18) ranged from about 4 to 15 mg/$\bar{g}$/day.

It appears, then, that food availability and not dissolved oxygen concentration limited the growth rates of the salmon in experiments where food availability was low. The rather strict dependence of growth rate

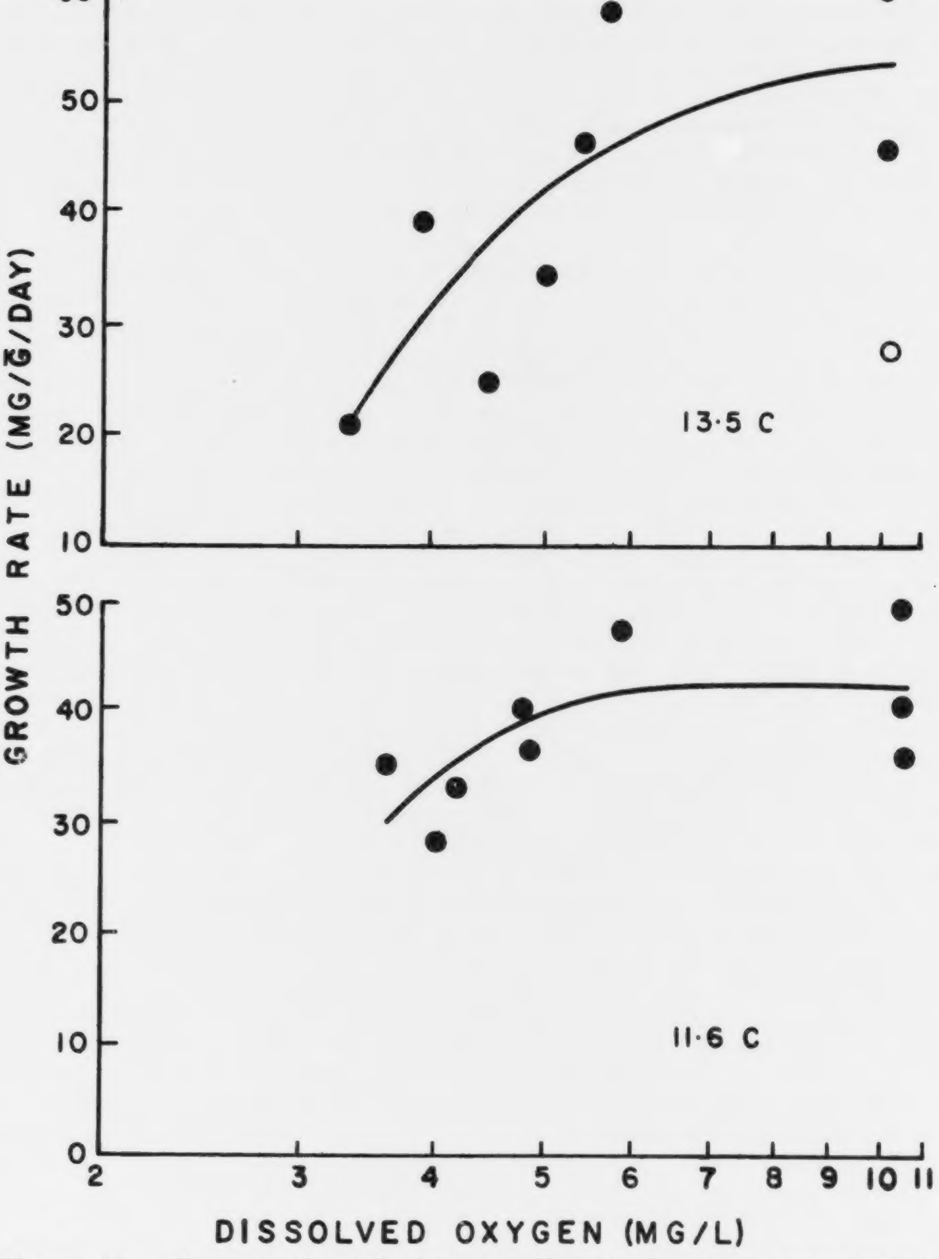


Figure 17. The relationship between dissolved oxygen concentration and growth rate of juvenile chinook salmon held for 10 days in the experimental streams in experiments 3 and 4. The open plot denotes test in which one fish was caught in export trap for up to 48 hours and may not have fully recovered.

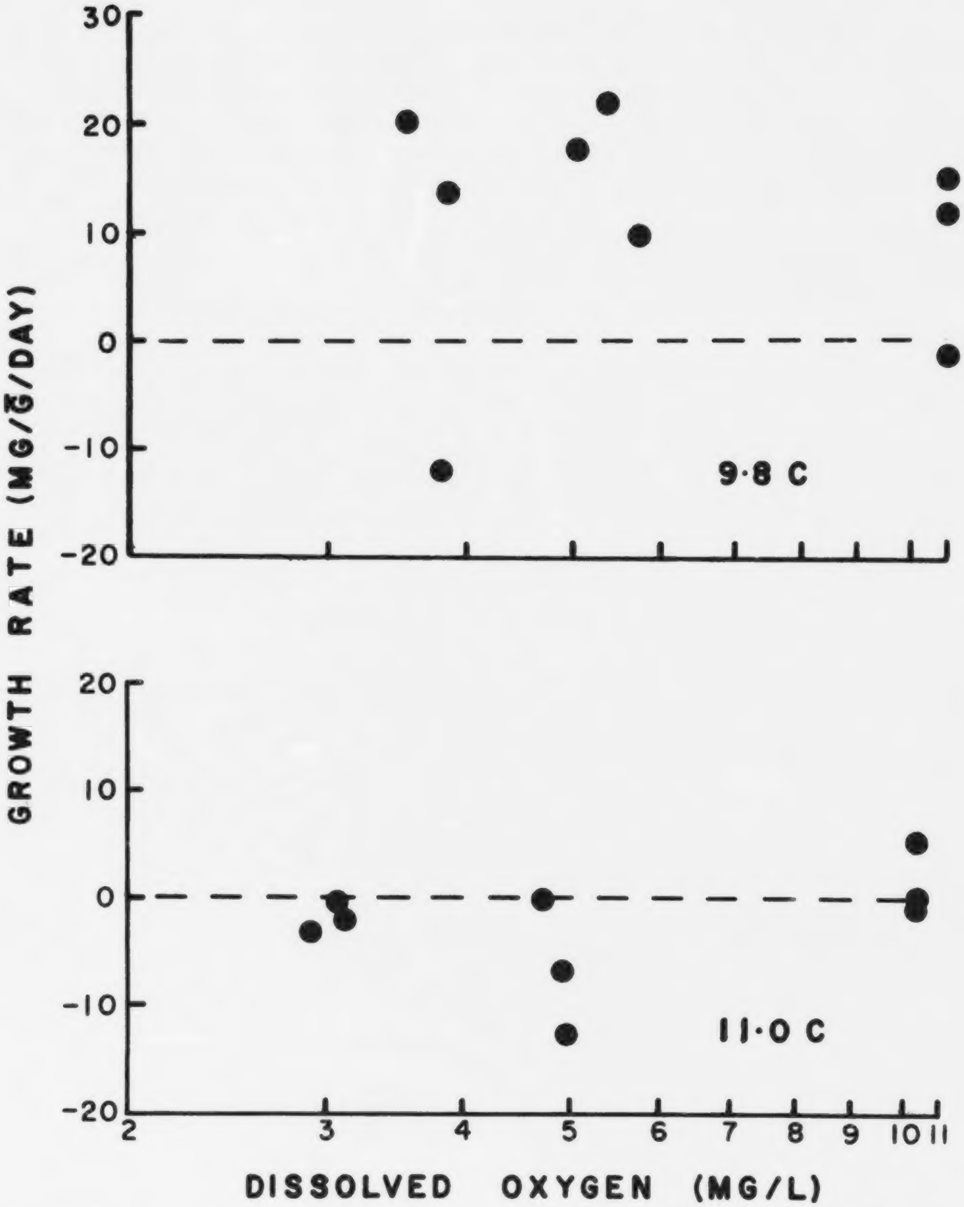


Figure 18. Relationships between dissolved oxygen concentration and growth rates of juvenile chinook salmon reared in the experimental streams for 10 and 20 days in experiments 2 and 8.

on food availability, at oxygen concentrations of 3 mg/l and above, when food is limiting is well illustrated in Figure 19, for experiments 2 and 7, which had low food levels.

But, our evidence indicates that when food availability is not limiting the growth of juvenile salmonids, their growth rate is dependent on dissolved oxygen concentration, so long as temperatures are favorable for growth. Under some conditions of food availability and temperature, any appreciable reduction of dissolved oxygen concentration below the air-saturation level is likely to reduce salmonid growth rates.

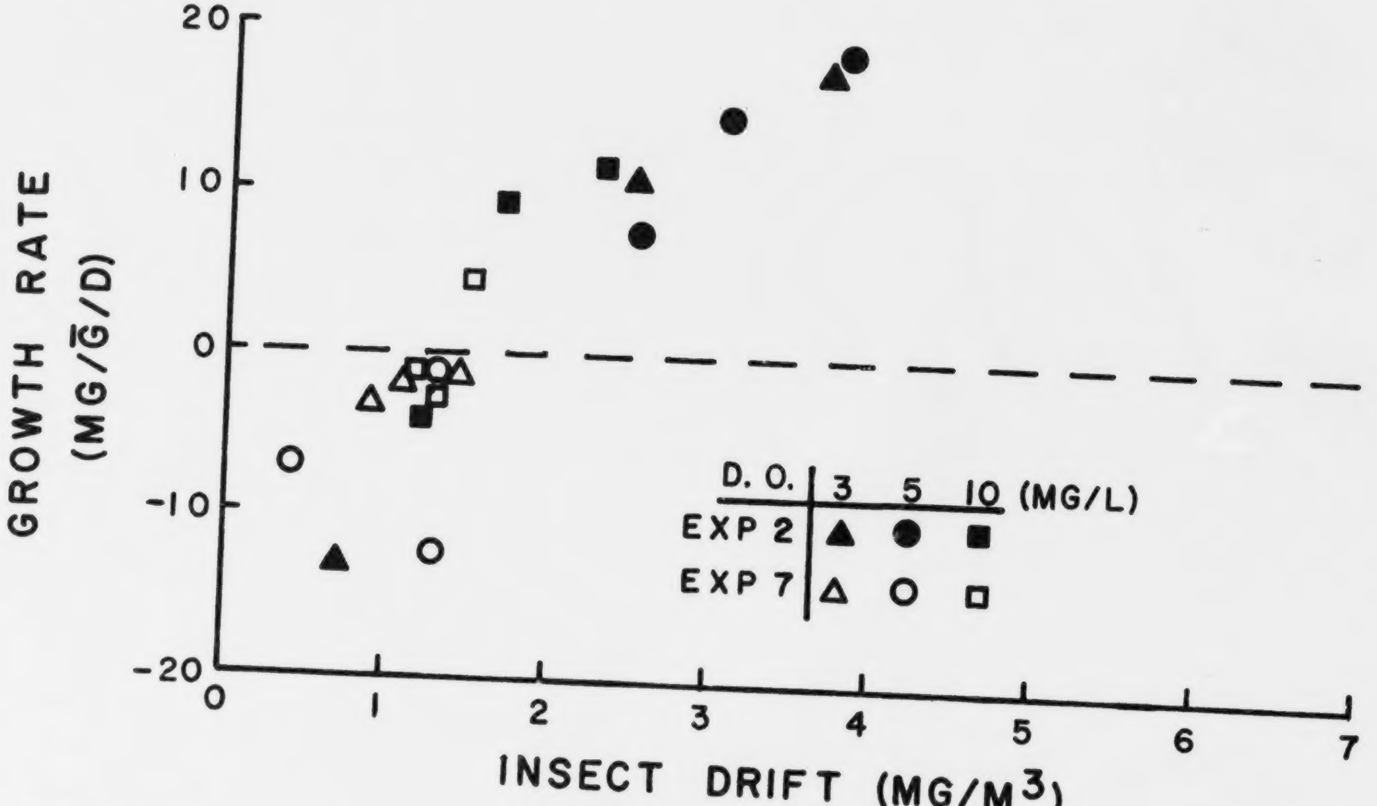


Figure 19. The relationship between food density and growth rate of juvenile chinook salmon held for 10 and 20 days in laboratory stream experiments 2 and 7, when food density was low and limiting food consumption and growth of the salmon.

SUMMARY OF RESULTS OF RESEARCH CONDUCTED FROM SEPTEMBER 1, 1955 THROUGH AUGUST 31, 1968 WITH SUPPORT FROM PREDECESSOR AGENCIES OF THE ENVIRONMENTAL PROTECTION AGENCY

INTRODUCTION

This terminal progress report nominally covers the methods, results, and interpretation of research we have conducted from September 1, 1968 through August 31, 1971, on the dissolved oxygen requirements of freshwater fishes. But the interpretation of these results and the recommendations as to dissolved oxygen criteria and needed research derive to a considerable extent from the results of research we conducted during the period from September 1, 1955 through August 31, 1968, with support from predecessor agencies of the Environmental Protection Agency. Although the results of this earlier work are reported in numerous publications and theses and have been reviewed by Doudoroff and Shumway (1970), we are here briefly summarizing this work for the convenience of those who must evaluate our recommendations. It may also be helpful to others to have in one place an overview of the results of our 16 years of research on the oxygen requirements of fish.

Very generally, this research has been concerned with the effects of decreases in dissolved oxygen concentration on the survival, avoidance reactions, swimming performance, embryonic development, and bioenergetics and growth of freshwater fish. During the last three years of this research, our entire effort on the project has been devoted to bioenergetics and growth. Thus, the work on the other problems was done prior to the period nominally covered by this progress report and will be included only in this section of this report, except as these results must be considered in discussing the more recent work, in making criteria and research recommendations, and in our general summary.

SURVIVAL

Studies on the survival of fish conducted during this investigation have been directed primarily toward determination of the influence of carbon dioxide concentration and pH on the oxygen requirements of juvenile coho salmon(*Oncorhynchus kisutch*). These studies were conducted largely in 1955 and in 1956 and have been reported in detail by McNeil (1956).

Evidence has been accumulated which indicates that temperature acclimatization, necessary activity, feeding status of the fish, and seasonal changes in the fish all influence the oxygen requirements of fish for survival. The influence of temperature on the minimal oxygen concentrations tolerated by coho salmon for periods of one to five days was studied prior to 1955. Davison et al. (1959) found that the 24-hour median tolerance limits (TL_m) for underyearling coho salmon 4-11 cm

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long exposed to constant O_2 concentrations in autumn did not increase at all with rise of temperature from 12 to 16C, the TL_m's remaining near 1.2 mg/l. These increased by only about 10 to 15 percent with increase of temperature to 20C. At higher temperatures, however, especially above 22C, the TL_m value rose steeply, being about 2.0 mg/l at 23.5C. McNeil (1956) observed 0 to 90 percent mortalities of juvenile coho salmon after 24 hours at nearly constant O_2 concentrations averaging 1.7 to 2.0 mg/l, temperatures of 20 to 22C, and free CO_2 concentrations of 3 to 20 mg/l, in summer. These data indicate perhaps an unusual susceptibility to O_2 deficiency of these fish that is considerably greater than that shown by the data of Davison et al. (1959). Data of Katz, Pritchard, and Warren (1959) show the 24-hour TL_m for juvenile chinook salmon at 20C to have been about 1.7 to 1.8 mg/l in summer and spring; and McNeil (1956) observed 50 to 70 percent mortality of juvenile steelhead trout at O_2 concentrations averaging 1.6 to 1.7 mg/l, temperatures of 16 to 20C, and free CO_2 levels of 3 to 8 mg/l, in late spring and early summer.

In experiments with coho salmon, Davison et al. (1959) observed few deaths of the animals after their exposure for more than 24 hours to O_2 concentrations that proved lethal to some of the fish in less than one day. Their tests were usually continued for five days, after gradual reduction of O_2 to constant levels in six to eight hours. They concluded that estimates of five-day tolerance limits would not have differed markedly from their estimates of 24-hour tolerance limits. In five-day tests with reticulate sculpins (*Cottus perplexus*), however, a number of deaths occurred after more than one day of exposure. Inasmuch as mortalities were recorded daily for exposure periods ranging from one to five days only, the relationship of survival time to O_2 concentration was not fully explored, and the true threshold of tolerance could not be established. It was suggested that the sculpin may have relatively limited acclimation capacity, as compared with coho salmon. The five-day TL_m for sculpins 4-7 cm in length at 18-19C was found to be near 1.5 mg/l, the recorded mortalities having been 40 percent at that oxygen concentration, 80 percent at 1.4 mg/l, and 0 percent at 1.6 mg/l dissolved oxygen, after five days of exposure. The 24-hour TL_m was about 1.3 mg/l, and the 48-hour TL_m about 1.4 mg/l.

In the studies of the influence of carbon dioxide and pH on the oxygen requirements of fish, the fish were held either in flowing-water apparatus or in sealed bottles. Oxygen concentration was controlled in the flowing water experiments by continuously replacing the water in the experimental chambers with water passed through columns having counter-current flows of nitrogen bubbles. The apparatus for the carbon dioxide and pH experiments was provided with means for continuously introducing carbon dioxide gas and sodium bicarbonate solution at the desired rates into the exchange flow of water. In the experiments with flowing water, the fish were gradually acclimatized to the desired experimental conditions, which were reached in the test chambers only after several hours; thereafter, constant conditions were maintained.

In the sealed bottle experiments, the fish were exposed to tested carbon dioxide and pH levels suddenly, but the periods of acclimatization to accompanying low oxygen levels were varied by varying the initial levels. There was a progressive decline of dissolved oxygen until all of the fish died, but the higher the initial level the longer was the acclimatization period. These experiments were conducted at a temperature of about 20C.

Preliminary flowing-water experiments with juvenile steelhead trout *(Salmo gairdneri)* and coho salmon indicated that carbon dioxide concentrations of 55 mg/l or less cause little increase of the minimum dissolved oxygen requirements of these species. Definitive experiments with coho salmon showed that in water having less than 5 mg/l of free carbon dioxide mean concentrations of dissolved oxygen varying from 1.7 to 2.0 mg/l are fatal to some but not all of the fish in 24 hours. Experiments in which the carbon dioxide concentration of the water was increased, but in which no bicarbonate solution was added and consequently the pH dropped to values ranging from 5.55 to 6.70, showed that a marked increase in the minimum dissolved oxygen concentration tolerated by coho salmon began at about 50 mg/l of carbon dioxide. Experiments in which the carbon dioxide concentration was increased and in which bicarbonate solution was added, so that pH values ranged from 6.35 to 7.25, showed a marked increase in the minimum dissolved oxygen concentration tolerated by coho salmon at concentrations of carbon dioxide above 80 mg/l. Though the coho salmon are able to tolerate lower levels of dissolved oxygen in the presence of high concentrations of carbon dioxide when the pH and total alkalinity are also high, it will be difficult to determine which of the latter two factors is the primary cause of this.

In sealed-bottle experiments in which coho salmon had little time to acclimatize to oxygen deficiency, a marked increase in the minimum dissolved oxygen concentration tolerated occurred at carbon dioxide concentrations less than 40 mg/l. On the other hand, when the initial oxygen concentration was high, so that a lethal level was not reached for a long time, such a large increase of the oxygen requirement occurred only at much higher carbon dioxide concentrations. Carbon dioxide appears to have much less effect on the tolerance of coho salmon to low levels of oxygen when the fish have been acclimatized to the high carbon dioxide levels for moderate periods before critical oxygen concentrations are reached.

In some sealed-bottle experiments, reductions in pH were made through the addition of sulfuric acid to the test water, and carbon dioxide liberated from the bicarbonates was removed by aeration. These experiments indicated that the levels of dissolved oxygen lethal for coho salmon do not vary materially within the pH range of 4.45 to 6.70, and that the levels lethal for bluegill sunfish (*Lepomis macrochirus*) do not vary significantly when the pH is between 4.0 and 7.5.

AVOIDANCE REACTIONS

Possible influences that low concentrations of dissolved oxygen and elevated concentrations of carbon dioxide might have on the movements of salmonid and centrarchid fishes were studied in the laboratory. Studies of avoidance reactions exhibited by fish confronted with waters of sharply different oxygen concentrations but nearly equal carbon dioxide concentrations were conducted during 1956 and 1957 and have been presented in detail by Whitmore (1957) and Whitmore et al (1960). Studies in which carbon dioxide concentrations were purposely varied, were conducted during 1957 and 1958 and have not been published as yet. The experimental results indicate rapid recognition and avoidance by some fish, notably salmonids, of water with reduced oxygen concentrations well above those known to be lethal for these fish. The observed avoidance of these oxygen concentrations by fish under the experimental conditions cannot be ascribed entirely to mere stimulation or increased activity caused by oxygen deficiency. It may not be assumed, however, that the same oxygen concentrations are usually avoided in the same way under more natural conditions.

The apparatus used for the avoidance reaction studies was a large tank into which opened four channels each measuring 6 inches wide and 36 inches long. Two of the channels received a continuous flow of water having reduced concentrations of dissolved oxygen and two received water having air saturation levels of dissolved oxygen. Special drains assured a sharp boundary condition at the channel entries. Avoidance indices were computed on the basis of the number of entries into channels, and on the basis of the number of times fish crossed a transverse line located well inside each channel, as well as on the basis of the numbers of fish observed in the channels at 60-second intervals. Based on one of the three different kinds of observations mentioned above, each avoidance index was computed by the formula:

$$\text{Avoidance index} = 100(M-A)/M$$

where M is the sum of the observations for all channels (experimental and control) divided by two, and A is the sum of the observations for the experimental channels only.

Studies were conducted on the avoidance reactions of juvenile chinook salmon (*Oncorhynchus tshawytscha*), coho salmon, largemouth bass (*Micropterus salmoides*), and bluegill (*Lepomis macrochirus*) to four concentrations of dissolved oxygen ranging from about 1.5 to 6 mg/l. All the species tested avoided some of the low oxygen concentrations, the degree of avoidance generally decreasing with increasing oxygen concentration. The chinook salmon avoided oxygen concentrations near 1.5, 3.0, and 4.5 mg/l, but they did not avoid concentrations near 6 mg/l, and they showed little avoidance of concentrations near 4.5 mg/l in the fall, when water temperatures were relatively low (near 12C). The avoidance of low concentrations generally was more pronounced in June and July, when water temperatures were high, than in the fall. The seasonal difference of the avoidance reactions was apparently primarily because of temperature differences.

Coho salmon in July avoided all tested oxygen concentrations at temperatures averaging 18.4 to 19C, but their reactions were more erratic than those of chinook salmon. Their avoidance of low oxygen concentrations was less than that of chinook salmon at corresponding temperatures, but the coho salmon showed some avoidance of concentrations near 6 mg/l, which were not avoided by the chinook salmon.

Largemouth bass markedly avoided 1.5 mg/l dissolved oxygen and showed slight avoidance of concentrations near 3 and 4.5 mg/l. Bluegill avoided oxygen concentrations near 1.5 mg/l rather markedly, and they apparently spent less time in channels with concentrations near 3 mg/l than in control channels. Channels with oxygen concentrations near and above 3 mg/l were entered almost as readily as control channels.

When the oxygen concentration was near the saturation level, juvenile coho salmon responded to differences in carbon dioxide concentration as low as 1 mg/l at temperatures around 20C, but at temperatures around 8C, they did not respond to differences as high as 30 mg/l. Some studies were directed toward evaluating the relative importances of elevated carbon dioxide and reduced dissolved oxygen in influencing the movements of juvenile chinook salmon in waters in which these conditions occur together. When tested separately at temperatures of about 18C, concentrations of about 2.5 mg/l of dissolved oxygen were avoided by some juveniles much more than were concentrations of about 15 mg/l of carbon dioxide. At about the same temperatures, older juvenile chinook salmon avoided carbon dioxide concentrations of approximately 35 mg/l about as much as they avoided concentrations of dissolved oxygen of approximately 2.6 mg/l. Juvenile chinook salmon showed much greater avoidance of water with carbon dioxide high (20 mg/l) and dissolved oxygen low (2.5 mg/l) than of water with both carbon dioxide and oxygen high or with both carbon dioxide and oxygen low.

SWIMMING PERFORMANCE

Studies of the swimming performance of fish were primarily directed toward determining the influence of dissolved oxygen and carbon dioxide on maximum sustained swimming speeds. Initial studies conducted during 1955, 1956, and 1957 were concerned with the ability of fish at low oxygen concentrations to swim at relatively low velocities for extended periods of time, and these studies have been reported in detail by Katz et al. (1959). The influence of dissolved oxygen on the maximum sustained swimming speed of coho and chinook salmon at different temperatures was studied during 1958 and 1959, and these studies have been reported in detail by Davis (1960) and Davis et al. (1963). During 1962, the influence of dissolved oxygen and carbon dioxide on the swimming speed of coho salmon and largemouth bass was investigated, these studies being reported by Dahlberg (1963) and

Dahlberg et al. (1968). Later studies conducted by E. M. Smith on the effects of reduced oxygen concentration on the length of time juvenile coho salmon can swim at very high velocities have been summarized by Doudoroff and Shumway (1967).

Juvenile coho salmon 95 to 124 mm in total length and chinook salmon 54 to 121 mm long, tested at 20C were able with few exceptions to swim for 24 hours against a current of 24.4 cm/sec at O_2 concentrations of 3.0 mg/1 or more. Largemouth bass 63 to 93 mm long, tested at 25C in September, were able to resist this current speed for 24 hours at O_2 concentrations near 2.0 mg/1. In December at temperatures of 15.5 to 17C, the bass were unable to resist this current when the O_2 concentration was reduced to 5.0 mg/1, although they were able to do so at concentrations near the air-saturation levels. The velocity of 24.4 cm/sec may, however, have been very near the maximum velocity that could be resisted in the well-oxygenated water at the relatively low experimental temperatures in December. In the other experiments with bass and salmon, the tested current velocity of 24.4 cm/sec doubtless was much below the maximum swimming speed that could be maintained for 24 hours by the fish in well-oxygenated water. The ability of the fish to swim at this speed at O_2 concentrations little higher than the lowest concentrations at which the fish can live under conditions necessitating no sustained activity is not evidence that there was little impairment of swimming capability.

The maximum swimming speeds sustained for ten-minute time intervals at different O_2 concentrations by coho and chinook salmon that were forced to swim at various temperatures against a gradually increased current usually declined with any considerable reduction of the O_2 concentration from the air-saturation level. The test temperatures in different experiments were from 10 to 20C. Increasing the O_2 concentration beyond the air-saturation levels had little or no favorable effect on the swimming performance of coho salmon. Largemouth bass tested at 25C showed impairment of the sustained swimming performance only when O_2 was reduced to levels below 5 or 6 mg/1. At the concentration of 3 mg/1, the final swimming speed of the bass was lower than the speed at the air-saturation level of O_2 by only about 10 percent. That of coho salmon tested at various temperatures was reduced by about 30 percent at this concentration (3 mg/1) and by about 10 percent at concentrations of 5 to 6 mg/1. Reduction of the swimming speed of the bass by 30 and 50 percent, from the speed at the air-saturation level of O_2, was found to occur at concentrations near 1.5 and 1.0 mg/1, respectively.

Doudoroff and Shumway (1967) mention some additional observations on the swimming performance of juvenile coho salmon at different O_2 concentrations made by E. M. Smith (unpublished data, Oregon State University). Smith observed a marked influence of O_2 on the length of time that the salmon swam against a suddenly accelerated current (previously of low velocity), which could be resisted by the fish for only half a minute to six minutes. Doudoroff and Shumway concluded that Smith's data suggest the possibility of less effect of dissolved oxygen on the duration of very rapid swimming than on the duration of less strenuous swimming.

In studies reported above, O_2 was removed from the water by means of nitrogen, so that free CO_2 concentrations did not increase as O_2 concentrations decreased, as they usually do under natural conditions. The maximum sustained swimming speeds of bass at 25C were not adversely affected at any O_2 level even by CO_2 concentrations averaging 48 mg/l (the highest concentrations tested) after overnight acclimation of the fish to the elevated CO_2 levels. The performance of coho salmon tested at 20C and high O_2 levels apparently was impaired somewhat by CO_2 concentrations averaging 18 mg/l, after overnight acclimation of the fish. The effect was greater when little time was allowed for adaptation of the fish to the elevated CO_2 level. Even after overnight acclimation, higher concentrations of CO_2 averaging 61 mg/l had a pronounced depressing effect on the final swimming speeds of the salmon at high O_2 levels. This effect decreased, however, as the O_2 concentration was reduced, and no effect was demonstrable at the 2 mg/l level. After overnight acclimation, 18 mg/l of CO_2 apparently had very little, if any, effect at O_2 concentrations near and below 6 mg/l, and none at levels below 3.5 mg/l. Free CO_2 concentrations much above 18 mg/l do not usually occur in waters that are not seriously deficient in O_2. One can conclude that the free CO_2 level is not generally an important consideration in deciding how much reduction of O_2 is likely to result in material impairment of the sustained swimming performance of coho salmon and largemouth bass in waters receiving organic wastes.

DEVELOPMENT

Salmonid embryos that are buried in streambed gravel depend on the movement of water through the gravel to supply them with the oxygen necessary for survival and growth and to remove metabolic wastes. Changes in the composition of the stream bottom can drastically reduce the rate at which this water is moving in the gravel and can lead to reduction of the concentration of dissolved oxygen and increase in the concentration of metabolic wastes. Such reductions of water velocity and oxygen content of the water can result in conditions within the gravel that are not conducive to survival, normal development, and good growth of salmonid embryos and fry. Even under conditions that are not lethal for embryos, delay of hatching and reduction in size of fry may result in poor emergence and survival. The above considerations have pointed to a need for detailed studies of the natural environments of salmonid embryos and experimental studies of the effects of specific environmental changes on their survival and growth.

Laboratory studies on the influence of dissolved oxygen concentration, metabolic wastes, and water velocity on the survival, growth, yolk utilization, and normal development of salmonid embryos and sac fry were conducted during this investigation. Early studies on the growth and survival of chinook salmon, coho salmon, and steelhead trout embryos were conducted from 1957 through 1959 and are reported in detail by Silver (1960), Shumway (1960), and Silver et al. (1963). Studies undertaken to define more completely the influence of water velocity and oxygen concentration on the growth, incubation time to hatching, and yolk utilization of coho salmon and steelhead trout embryos are reported in detail by Shumway et al. (1964) and Chapman (1969). The influence of metabolic wastes on development and growth of salmonid embryos and larvae are reported in detail by Putnam (1967), and further studies of the influence of oxygen concentration and water velocity on the growth of alevins and the time of complete yolk sac absorption are summarized by Doudoroff and Shumway (1967).

The apparatus used for these studies was designed to provide developing salmonid embryos and sac fry with a constant rectilinear flow of water having independently controlled velocities and oxygen concentrations and uniform temperature. With this apparatus, which was located in a constant-temperature room, it was possible to test four different water velocities at each of six different oxygen concentrations during a single experiment. Several hours after fertilization, 60 to 140 eggs from a single female were placed into each of the test cylinders within the apparatus, the number of eggs being the same in all cylinders during any single experiment. The water velocities and oxygen concentrations to be tested were then established and maintained until the termination of the experiment. Removal of dead material, or sampling of live material, was possible. Wet and dry weights were usually determined, rather than volumes, as it was found by comparison that either the wet or the dry weights, and especially the dry weights, could be far more precisely determined than the volumes. Both volumes and wet weights were determined after the yolk and excess water had been removed, and the embryos with yolk removed were dried to constant weight for the dry weight determination.

Under laboratory conditions, good survival of embryos of steelhead trout and coho and chinook salmon has been repeatedly observed when eggs were exposed--continuously from the time of their fertilization until hatching--to mean O_2 concentrations as low as 2.5 to 3.0 mg/l at temperatures of 9 to 11C. Embryo mortalities were often greater and deformities tended to occur more frequently at these low O_2 concentrations than at higher concentrations, but hatching proved impossible only at tested concentrations below 2.0 mg/l. Survival of chinook salmon and steelhead trout embryos at concentrations averaging 2.6 and 2.5 mg/l was equal to that of controls, and 100 percent success in hatching chinook salmon eggs (at 11C) was observed at concentrations averaging 3.9 mg/l.

Any considerable reduction from air-saturation levels (i.e., even to levels as high as 8 or 9 mg/l) of the O_2 content of water in which the embryos were reared at various water velocities resulted, however, in some reduction in size of the newly hatched larvae (alevins). Mean weights--determined after removal of the yolk--of coho salmon, chinook salmon, and steelhead trout alevins at the time of hatching at O_2 levels of 2.5 to 3.0 mg/l were about one-fourth to one-half of those of controls reared at levels near air-saturation. The dry weights of coho salmon alevins (with yolk sac removed) hatching at O_2 concentrations that averaged 2.8, 3.8, 4.9, 6.5 and 8.6 mg/l in an experiment at 10C were less than those of the controls (at 11.2 mg/l) by about 70 percent, 59 percent, 40 percent, 20 percent and 5 percent, respectively. These percentages are means of values obtained at four different water velocities. Mean dry weights of steelhead trout alevins hatching at O_2 concentrations that averaged 2.9, 4.1, 5.7, and 8.0 mg/l were less than those of controls (at 11.4 mg/l) by about 56 percent, 36 percent, 21 percent, and 7 percent, respectively, on the average, in two like experiments at 10C and 300 cm/hr water velocity.

Studies on the three species of salmonids have shown that reductions in velocity of water passing the embryos can result in reduction in size of the embryos at the time of hatching. Water velocities tested in different experiments were from 3 to 1400 cm/hr. The favorable effect of increased water velocity on the size of hatching larvae apparently is ascribable for the most part, if not entirely, to improved delivery of O_2 to chorion surfaces. Increases of water velocity that had this effect did not, however, always result in appreciable shortening of incubation periods required for hatching, especially at high and only moderately reduced O_2 concentrations. In addition to delivery of O_2, removal of some metabolic products, which likewise can influence development, also may be involved. The influence of water velocity is not nearly as pronounced as is the influence of oxygen concentration; the influence of water velocity is, however, nearly as great at high oxygen concentrations as it is at low concentrations.

Reduction in oxygen concentration resulted in a delay in hatching of the salmonid embryos. In a typical experiment with coho salmon embryos, the delay of hatching is taken to be the difference in days between the median hatching time for fry reared under the various test conditions and 44 days, which was the median hatching time recorded under the most favorable experimental conditions tested in the experiment. Any reduction of oxygen concentration resulted in delayed hatching of fry at all water velocities, the greatest delay occurring at the lowest oxygen level tested (2.8 mg/l), where the delay was 11 days. However, a reduction of water velocity from 800 to 3 cm/hr did not cause any delay of hatching at the highest oxygen concentration (11.2 mg/l). Also, there was not much delay attributable to reduction in water velocity at oxygen concentrations of 8.6 and 6.5 mg/l. At lower oxygen concentrations, a more pronounced effect of water velocity on hatching time was observed.

Metabolites produced by a large mass of developing embryos slightly inhibited growth of steelhead trout embryos but did not inhibit growth of sac fry. An ammonia concentration of 5 mg/l and carbon dioxide concentrations above 28 mg/l were also found to inhibit embryonic growth. But the water passed through the mass of developing embryos before being introduced into the chamber holding the experimental embryos contained only 0.1 mg/l or less of ammonia and 3 to 6 mg/l of carbon dioxide. Thus, such growth inhibition as occurred must have been primarily owing to other metabolites. These and other results lead us to conclude that oxygen concentration rather than metabolites are most important in affecting embryonic development and that water velocities sufficient for oxygen delivery are more than sufficient for metabolite removal.

The maximum dry weights attained by unfed salmonid alevins at reduced O_2 concentrations were reduced only moderately (by about 25 percent or less) or were nearly equal to those of controls, by the time yolk sac absorption was complete. These maximum sizes were attained at the reduced concentrations usually with some delay, up to maxima of about 18 days (25 percent) for steelhead trout and 30 days (35 percent) for coho salmon. The stated results were obtained at mean O_2 concentrations even as low as 2.9 to 3 mg/l, in experiments in which the alevins were reared at temperatures near 10C and a relatively high water velocity (300 cm/hr). When both the O_2 concentration and the velocity of water movement around the alevins were very low (O_2 about 3 mg/l; velocity about 10 cm/hr), the growth of the alevins was much impaired. Mortalities of the alevins then were relatively high, and nearly complete absorption of yolk had not yet been attained by the surviving ones when the experiments were discontinued. It was evident, however, that had the experiments been prolonged, the maximum size attained by the unfed, surviving alevins would have been much less than that of controls reared at the low water velocity but at a high O_2 level. Chinook salmon alevins appeared to be affected by these adverse conditions more than were the other species tested. Reduction of dissolved O_2 to about 5.6 mg/l had, however, very little effect on their growth and on that of the other species even at the low water velocity of 10 cm/hr. Exposure of developing embryos to a very low O_2 level until hatching had no appreciable adverse effect upon the rate of subsequent growth of alevins returned to a high level of O_2.

BIOENERGETICS AND GROWTH

Although our studies on the influence of dissolved oxygen on the growth of juvenile coho salmon began in 1955 and those on the growth of largemouth bass began in 1961, the more bioenergetic aspects of our growth studies were not undertaken until 1964. From 1964 through 1968, bioenergetic studies of coho salmon and bass and studies of bass in experimental ponds--where conditions were more natural than in the more typical laboratory studies--were undertaken. The earlier studies on growth were mainly concerned with the influences of dissolved oxygen when food availability was largely unrestricted, but two experiments were performed in which coho salmon were fed low restricted rations. Nearly all the above mentioned studies are reported in detail in the following series of theses and publications: Herrmann (1958), Herrmann et al. (1962), Fisher (1963), Stewart (1962), Stewart et al. (1967), and Lee (1969).

Decreases in the growth rates of juvenile coho salmon and largemouth bass with decreases in oxygen concentration from the air-saturation level to 3 or 4 mg/l can be attributed mainly to decreases in appetite and food consumption, when largely unrestricted rations were fed. When restricted rations were fed, there was little or no difference in the growth of the salmon at oxygen concentrations ranging from 3 or 4 mg/l to the air-saturation level.

In laboratory experiments at temperatures of 18 and 20C, the growth rates of underyearling coho salmon--fed largely unrestricted rations of amphipods or tubificid worms--tended to decline with any reduction of O_2 from the air-saturation levels, which are near 9 mg/l. The results of those experiments that were deemed fairly reliable indicate decreases of growth rates (based on wet weights) averaging about 8 percent, 17 percent, and 42 percent (30 percent in the three experiments at 18C) at O_2 levels of 5, 4, and 3 mg/l, respectively. These percentages are means of estimates that we derived by calculation of the growth rates and graphical interpolation.

A rather abrupt change in slope, at about 4.5 mg/l O_2, of the curve relating percent gains in weight to the O_2 concentrations was indicated by the results of one group of experiments, in which the fish were fed amphipods twice daily. We have found, however, that when growth rates of the fish are plotted against logarithms of O_2 concentrations a smoother curve fits the data well. In similar subsequent experiments performed at 18C, live tubificid worms were used mainly as food, and the live food was available to the fish continuously. The growth at high O_2 levels in these experiments with unrestricted rations was faster than it was in the earlier tests, and smooth curves relating the growth rates to the logarithms of O_2 concentration were easily fitted to plotted data. The slope of these curves decreased, but not abruptly, as the O_2 concentration increased to and beyond the air-saturation level. At O_2 levels of 30-35 mg/l, very far above the air-saturation level, growth rates were less than maximal, but were depressed by only about 4 percent on the average, as compared with growth at the air-saturation level. The optimum for growth when rations are unrestricted appears to be about 12 to 15 mg/l. However, in one additional experiment, virtually equal growth rates were observed at O_2 concentrations near 6 and 12 mg/l. This result indicated an optimum near the air-saturation level.

Food consumption rates of underyearling coho salmon declined, as did their growth rates, with reduction of O_2 from levels near saturation levels in the experiments at 18 and 20C. The gross efficiency of food conversion tended to be considerably reduced only when food consumption was very low because of much reduced O_2 concentrations (i.e., somewhat below 4 mg/l in all experiments whose results were deemed reliable). In several tests at mean O_2 levels of 2.0 to 2.3 mg/l, consumption of intermittently available food was extremely reduced and the fish lost weight. In two experiments performed in May and June at 18C, however, underyearlings that were fed unrestricted rations of tubificid worms consumed enough food to grow moderately well at mean O_2 levels of 2.4 and 2.5 mg/l. Their growth rates were reduced, as compared with those of controls, by about 45 percent; this value can be compared with a reduction by about 30 percent at the 3.0 mg/l level of O_2 observed in the same and in entirely similar experiments at 18C. The coho salmon in these experiments obviously would have gained some weight at concentrations well below 2.4 mg/l, if not below 2.0 mg/l. Thus, the results of all the pertinent tests considered together indicate that average O_2 concentration at which underyearling coho salmon can just maintain their weight without growing when they are offered abundant food rations at temperatures of 18 to 20C is not much above 2.0 mg/l.

An experiment in which groups of juvenile coho salmon of nearly equal initial weight were fed equal rations of tubificid worms at 18C and at six different, constant O_2 concentrations ranging from 3 to 18 mg/l was conducted. Each group of fish received only as much food as could be readily consumed by the fish held at the lowest O_2 level. Reduction of O_2 to 4 mg/l had no evident effect on the growth of these fish. At the 3 mg/l level, the fish grew a little less than did the fish at the higher concentrations. Gains in wet and dry weights and in crude fat all proved nearly independent of the O_2 concentration. In a similar later experiment, in which the lowest O_2 level was 2.3 mg/l and rations were correspondingly reduced, no impairment of growth was observed even at this very low concentration. It is evident that coho salmon consuming equal amounts of food utilized this food for growth about as efficiently at the much reduced O_2 concentrations (certainly at concentrations as low as 4.0 mg/l) as they did at higher concentrations.

Six experiments in which groups of juvenile largemouth bass were fed earthworms at temperatures near 26C and at different, nearly constant O_2 concentrations (1.6 to 24 mg/l) were conducted. The worms were available to the fish at all times. Food consumption and growth rates of the bass clearly tended to be reduced by any considerable reduction of O_2 from levels near the air-saturation level, which is about 8 mg/l. The optimal concentration appeared to be very near the air-saturation level; at levels much above saturation both food consumption and growth rates tended to be depressed. The indicated decreases of the growth rates of the bass (from the rates of growth at the air-saturation level of O_2) at reduced O_2 concentrations of 5, 4, 3, and 2 mg/l averaged about 8.5 percent, 16.5 percent, 30 percent, and 52 percent, respectively. These values are means of estimates that we derived by graphical interpolation from the results of five of the six experiments, disregarding one experiment, the results of which were deemed too erratic. The gross efficiency of food conversion by the bass usually was considerably impaired at O_2 levels below 3 or 4 mg/l, and nearly independent of O_2 at higher levels. The bass invariably gained weight or were evidently capable of growing at an O_2 concentration of about 2 mg/l; concentrations considerably lower than this (but not as low as 1.0 mg/l) apparently would not usually have prevented growth entirely. The average depression of growth rates at excessive O_2 concentrations averaging 20 mg/l in three experiments was about 11 percent.

The growth of juvenile coho salmon and largemouth bass kept on unrestricted rations at widely fluctuating O_2 concentrations was markedly less than their estimated growth at constant concentrations equal to the means (arithmetic and geometric) of the fluctuating concentrations. The fish were subjected daily to high and low concentrations, usually for equal periods following periods of gradual transition; low concentrations occurred at night and early in the morning. Mean limits of the O_2 fluctuations in the experiments with coho salmon were 2.3 and 9.6, 3.0 and 9.5, 3.0 and 18, 4.9 and 35.5 mg/l. In the experiments with largemouth bass, the mean lower limits were usually about 2 mg/l and the upper limits were usually about 6, 8, or 17 mg/l. Weight gains that would have occurred at intermediate constant concentrations were derived for comparative purposes by interpolation from results of simultaneous tests at several constant concentrations, including concentrations near the limits of the tested fluctuations. The growth of the fish subjected to diurnally fluctuating concentrations often proved equivalent to that which would have occurred at constant levels only a little above the lower limit of the wide fluctuations. Their food consumption rates were correspondingly depressed.

As we have noted, when food is not limiting, any reduction in the concentration of dissolved oxygen below the air-saturation level can be expected to reduce the rate of food consumption of fish, unless low temperatures are leading to low consumption rates. The rate of food consumption of juvenile coho salmon, forced to swim at constant low velocity was found to increase with increasing oxygen concentration. Growth rate increased slightly with increasing availability of oxygen, but not so much as food consumption rate, because respiration increased, primarily as a result of increased specific dynamic action. It was the ability of the fish to increase their rate of respiration with increase in oxygen availability that permitted consumption rate and, in consequence, growth rate to increase. Oxygen, here, was acting as a limiting factor.

Not only very high levels of food consumption but also very high levels of activity can lead to oxygen acting as a limiting factor, even at air-saturation levels of oxygen. Juvenile coho salmon were found to reduce their food consumption rate to make oxygen available for swimming at the increased velocities. Reduction in the energy cost of food handling thus permitted increased energy utilization for activity, even though respiration rate remained constant.

Oxygen consumption rates of juvenile coho salmon and largemouth bass tended to decline with any reduction of dissolved O_2 below the air-saturation levels. We have reported already that the food consumption and growth rates of the fish likewise were dependent on the O_2 concentration at all levels below the saturation level. Some pertinent observations incidental to already reported experiments on the growth of coho salmon that were fed uniform, restricted rations at 18C at various O_2 concentrations have been examined. These data indicate no dependence of O_2 uptake rates on O_2 concentration over the wide range of concentrations that had no demonstrable influence on the growth rates of the fish, from the air-saturation level to 4 mg/l or less. No dependence was to be expected in this case, because ration size was equally restricted at all O_2 levels tested.

Results of the preliminary experiments in the experimental ponds indicate that, over a wide range of prey densities, the metabolic rate of largemouth bass preying on mosquitofish, *Gambusia affinis*, which were usually provided suitable escape cover, did not vary much with changes in prey density. The food consumption and growth rates of the bass increased with increasing prey density over the entire range of densities tested. Yet, at the moderate test temperatures, averaging about 21C, the average metabolic rate--determined by the energy-balance method--apparently remained nearly constant at about 26 calories per kilocalorie of bass tissue per day. The apparent constancy of the metabolic rate of the bass indicates that, as the availability of food and the rate of food consumption increased, so that more energy was required for the cost of food handling, the activity of the bass decreased. In other words, a decrease of the expenditure of energy for activity apparently compensated for the increase of the so-called "specific dynamic action" of the food that was consumed in increasing amounts as the density of prey increased. This conclusion was in accord with visual observations. When the prey density was high, or when the escape cover for the mosquitofish was removed, the bass often were able to capture their prey with relatively little effort. When food was less abundant, they evidently expended more energy in seeking the prey and pursuing it, usually failing to capture it.

There are reasons for believing that the dissolved O_2 concentration, which was near the air-saturation level in these experiments with bass, may have determined the metabolic rate of the bass, thus limiting their activity and food consumption. It was found that, at 20C and O_2 levels near air-saturation, the metabolic rate of more rapidly growing largemouth bass kept in aquaria on unrestricted rations of unprotected and easily captured mosquitofish was not materially different from that of the bass in the ponds. This observation suggests that the average metabolic rates of these fish at the same temperature in nature are not much lower or higher, and that critical levels of O_2 may be about the same in nature as they are for fish fed unrestricted rations in the laboratory at the same temperature. We have already reported that the food consumption, growth, and O_2 uptake rates of largemouth bass that were kept on unrestricted rations in laboratory aquaria at about 20 and 26C tended to decrease with any considerable decrease of dissolved O_2 from the air-saturation level. This finding definitely indicates restriction of the metabolic rate of the abundantly fed bass at 20-26C by the availability of O_2 even in nearly air-saturated water. One can conclude that the apparently not very different metabolic rates of bass in the ponds also may well be oxygen dependent at O_2 levels near the saturation level.

GENERAL DISCUSSION

We shall here consider mainly possible relations between our laboratory findings and effects of reduced dissolved oxygen concentrations on the well-being and production rates of populations of fish in nature.

Our data on avoidance reactions of fish to low oxygen concentrations under the highly artificial test conditions are of some physiological interest and suggest--as does also the distribution of fish in nature--that fish in their natural environment will not avoid all reduced oxygen concentrations that are likely to impair their performance or physiological functions. No conclusion can, however, be reached as to the concentrations that are avoided in natural situations where transition from high to low oxygen concentrations is not nearly as abrupt as that in our experimental tank.

The demonstrated reduction of maximum sustained swimming speeds of salmonid fishes by only slight reduction of dissolved oxygen concentration from air-saturation levels may be important in some natural situations. But very rapid swimming for short intervals of time is probably more often required in nature than is prolonged swimming at maximum speeds sustainable. The influence of dissolved oxygen on "burst" speeds that are maintainable only for fractions of a minute and on the frequency with which such burst swimming can be repeated has not been investigated. There are physiological reasons for doubting that reduced oxygen concentrations have as much influence on burst speeds as on maximum sustainable speeds.

The observed reduction in size of salmonid alevins hatching from eggs exposed continuously to low oxygen concentrations at moderate to high water velocities and the delay of their hatching may or may not materially influence their ability to survive in stream-bed gravels and after emergence from these gravels. By the time of complete absorption of the yolk sacs of fry reared at high and low oxygen concentrations at which the eggs were incubated and hatched, the size differences are not nearly so pronounced. But substantial differences in maximum sizes attained by fry, reduced rates of growth, and much higher mortality rates were observed at moderately reduced oxygen concentrations when salmonid embryos and fry were held at low water velocities, such as are common in streambed gravels. Failure of salmonid embryos and alevins to survive at favorable temperatures in heavily silted stream-bed gravels where oxygen concentrations are only moderately reduced cannot always be attributed only to oxygen deficiency in the water moving through the gravels, because silt may impair oxygen movement across the chorions of the eggs, and in other ways influence the alevins. In laboratory experiments, only low oxygen concentrations when water velocities were low proved fatal or prevented attainment of nearly normal size of alevins. Nevertheless, even under entirely natural conditions, oxygen concentrations in riffle-bottom gravels are not everywhere sufficient for successful development of salmonid fishes, and any reduction of oxygen concentrations in water flowing over and through the gravels must result in some reduction of stream-bottom areas suitable for salmonid spawning.

We can now turn to discussion of the results of our experiments on the influence of dissolved oxygen on the growth of juvenile fishes under various conditions, the main subject of our investigations of the last three years of the overall study.

There is no indication that the effects of reductions of oxygen concentration on the growth of largemouth bass feeding more or less naturally on mosquitofish in our artificial ponds are very different from the effects on the growth of these fish in laboratory aquaria when they are fed unrestricted rations. At temperatures near 19C (18-20C), agreement between the percentages by which growth rates of bass feeding on mosquitofish were reduced upon reduction of the oxygen concentration to the same mean level (4.3-4.4 mg/l) in the ponds and in aquarium tests was excellent (about 20 percent reduction in each case). In both the pond and aquarium tests at temperatures around 13C (13-14C in ponds, 10-15C in aquaria), similar reductions of oxygen concentration had very little or no effect on the growth rates of the largemouth bass. There are reasons for supposing that the observed impairment of growth in the ponds by reductions of oxygen concentration at temperatures of 16-17C were greater than those that would have occurred in the aquarium tests, but no aquarium tests at these temperatures were performed. Also, at temperatures between 23 and 28C, the impairment of growth in the ponds at reduced oxygen concentrations appeared to be somewhat greater than that found to occur in the aquarium tests at the same oxygen concentrations. But the difference of these results could well have resulted from experimental error.

The influence of food availability, or food-organism density, on the degree of depression of growth rates of bass in the ponds at reduced oxygen concentrations has not been adequately evaluated. In three experiments at about 18-19C in which the food-organism density was varied, the greatest depression of growth rate at reduced oxygen concentrations was observed when the food density was highest. The difference between the results obtained at the two lower food-organism densities was negligible. The noted good agreement between the results (percent depressions of growth rates) obtained in the pond tests and the aquarium tests in which food consumption and growth rates of the bass were much greater than they were in the pond experiments indicates that food availability may have had little or no influence on these results. This conclusion is indirectly supported by the available bioenergetic data, which indicate that the metabolic rate of the bass in the ponds was independent of food-organism density. If metabolic rates remain constant, the dissolved oxygen requirement for unimpaired growth of the fish also should be constant, and the degree of impairment of growth by a given, large reduction of dissolved oxygen presumably also should not vary greatly. On the basis of the above considerations, it now appears that the effects of dissolved oxygen reduction on the growth of largemouth bass in their natural environments can be fairly reliably predicted from the results of simple aquarium tests in which food rations are unrestricted.

The degree of impairment of the growth of juvenile chinook salmon in the laboratory streams upon reduction of the oxygen concentration to a given low level varies widely with the availability of food. Therefore, close correspondence between the results of laboratory stream tests, in which different relatively low levels of food availability are maintained, and those of aquarium tests in which food rations are unrestricted cannot be expected at all temperatures. But at the relatively low temperatures of our laboratory stream experiments, the critical dissolved oxygen levels below which growth was oxygen-dependent in the streams having higher levels of food availability were not markedly different from the critical levels determined in aquarium experiments with unrestricted food rations at similar low temperatures. No laboratory stream experiments were performed at relatively high temperatures at which the growth rates of juvenile chinook salmon in aquarium tests, as well as those of coho salmon, proved dependent on oxygen concentration at all concentrations below the air-saturation level. It appears that, at the higher temperatures at least, the effects of dissolved oxygen reductions on growth in the laboratory streams with low to medium levels of food availability should be less pronounced than the effects observed in laboratory aquarium tests with unrestricted food rations.

The dependence of the critical level of dissolved oxygen on food availability that has been observed in the experiments with laboratory streams, however, does not necessarily exist in nature. In the laboratory streams, the salmon feeding on drifting organisms probably could gain little when food availability was low by exerting themselves more than they did when food was relatively abundant. We cannot safely assume that the same is true in nature, where, when food is scarce, it may be advantageous for young salmon to expend more energy in exploiting stream resources. A competitive advantage perhaps could be gained by maintaining a nearly maximum metabolic rate, whatever the level of food availability. Then, any reduction of oxygen concentration would result in reduction of food consumption and growth rates, and the impairment of growth could be similar to that observed at the same oxygen concentration and temperature in aquaria with an unlimited and readily available food supply. Only further research can reveal to what extent the depression of growth rates of salmon by reduction of dissolved oxygen in laboratory aquaria is indicative of the depression that would occur in the laboratory streams and in nature at the same temperature.

SUGGESTIONS CONCERNING WATER QUALITY CRITERIA FOR PROTECTION OF FISHERIES

Water quality criteria and standards can be designed for the protection of particular species, or even of particular populations, of fish deemed of sufficient economic or recreational importance, when adequate information is available on the environmental requirements of those species or populations. Such specific criteria and standards have obvious advantages over those pertaining to fish in general. Unfortuantely, however, reasonably complete information on the dissolved oxygen requirements of only a few important fish species is now available. And convincing evidence that these requirements are adequately representative of those of major taxonomic groups or ecological types to which the particular species belong is also lacking. An alternative approach to the development of water quality criteria involves consideration and synthesis of all available information on the relations of fishes in general to particular environmental factors, with careful attention to general biological principles.

Faced with the task of devising dissolved oxygen criteria to be recommended for worldwide application, Doudoroff and Shumway (1970) had no choice but to adopt the latter approach. Their recommendations, based on a comprehensive survey of the pertinent world literature, as well as on all the data available in our laboratory at the time of preparation of their publication, are reprinted in Appendix III of this report. But here we shall discuss in some detail only the possibilities pertaining to the first-mentioned approach, inasmuch as most of our data have to do with only a few fish species whose dissolved oxygen requirements we have intensively investigated. The reader must decide for himself whether or not, or to what extent, conclusions or criteria based on the research into the requirements of certain populations of these species are to be regarded as applicable to other species, or to other populations of the same species, whose requirements have been investigated little or not at all. We need not take any position here with regard to the advisability of such general application of specific information, in our present state of knowledge.

As noted by Doudoroff and Shumway (1967, 1970), water quality criteria can be designed for total protection of valuable fish populations, admitting virtually no impairment or risk of impairment of fish production, or they can be designed for various lower levels of protection of fisheries that would merely limit the impairment of production. Realizing that different levels of protection of fisheries may be appropriate under different circumstances, Doudoroff and Shumway (1970) proposed different dissolved oxygen criteria that they deemed appropriate to several different levels of protection described by them (see Appendix III). These criteria pertain to freshwater fish populations in general, but criteria designed for the protection of particular species likewise can provide for more than one level of protection. We are now ready to consider criteria that may be appropriate for

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different levels of protection of those particular fishes that we have instensively studied.

Table 1 shows the lowest level of dissolved oxygen at which each of a variety of responses of fish to reduction of oxygen concentration does not appear to us to have proved demonstrable under the specified experimental conditions. It can be seen from this summary of our findings that, while some presumably undesirable effects of dissolved oxygen reduction were apparent only at relatively low oxygen concentrations, other effects or responses were demonstrable upon any considerable reduction of dissolved oxygen from the air-saturation values, at least at moderately elevated temperatures. Specifically, some of the latter responses are: reduction in hatching size of salmonid embryos, delay of hatching of salmonids, reduction of maximum sustained swimming speeds of salmonids (but not of largemouth bass), and reduction in growth rates of coho salmon fed unrestricted rations in aquaria and of largemouth bass fed unrestricted rations in aquaria as well as feeding more naturally in artificial ponds. These findings lead inevitably to the conclusion that any considerable reduction of dissolved oxygen below saturation levels is likely to have some adverse effect on the functions or performance of the fish species studied and, therefore, on their production rates under natural conditions, except perhaps at low temperatures unfavorable for growth.

But let us now grant that some limited impairment of fish production rates, say a reduction by no more than 20 percent, often must be and will be accepted in establishing dissolved oxygen criteria or standards for moderate protection of fish populations. Can the lowest dissolved oxygen level at which the impairment of production would not exceed this maximum acceptable impairment be estimated? If so, on what kinds of data should such estimates be based?

We can offer no justification whatsoever for the assumption that a 20 percent reduction of the maximum sustained swimming speed of a fish, or a 20 percent reduction of the size of its embryos at the time of hatching, or a 20 percent delay of hatching, would usually result in a reduction of the production rate of that fish in nature by about 20 percent, or by any other particular (more or less predictable) percentage. On the contrary, there are good reasons for believing that such moderate effects of dissolved oxygen reduction would not, by themselves, usually result in any appreciable impairment of production. Prolonged swimming at nearly maximum sustainable speeds is not often required of fish in nature. Moderate reduction of hatching size has not been found to result in a corresponding reduction of the size attained by salmonid larvae by the time of complete absorption of the yolk sac. Even some reduction in size of the emerging fry should not result in increased competitive disadvantage for any of them if the reduction is uniform. Spawning seasons of fish usually are fairly extended, and hatching time can vary more widely with natural variations of temperature than with moderate variations of oxygen concentration. Generally, many more young fish are produced than can survive and grow to maturity,

Table 1. The responses of various species of fish held under laboratory conditions to reductions of dissolved oxygen concentration. The letters H (saturation or above), I (>4.0 mg/l, but much less than saturation), and L (<4.0 mg/l) indicate the highest level of dissolved oxygen at which the indicated response changed. The temperatures at which the various experiments were conducted are close, but not identical to those shown in the table headings.

Response	Coho salmon				Largemouth bass					Chinook salmon			Steelhead trout			Bluegill	Sculpin
	Temp. degrees C				Temp. degrees C					Temp. degrees C			Temp. degrees C			Temp degrees C	Temp. degrees C
	10	15	20	>21	10	15	20	25	30	10	15	> 20	10	15	20	20	18-19
Juvenile sustained swimming speed	I-H	H	H					I		H	H						
Development[1/] (size at hatch)	H									H	H		H				
Larval[1/] growth (max. size attained)	H									L-I			I-H				
Hatching success	L									L			L				
Survival[1/] through yolk absorption										L	H						
Delay in hatching	H									H	H		I-H				
Avoidance			I[2/]				L				L	I				L	
Juvenile death	L	L	L	L	L	L	L	L	L	L	L	L				L	L
Juvenile growth (aquaria)	I-H	I-H	H	I-H	L	L	H	H	H	L-I	I	H					
Juvenile growth (ponds)						L	I[2/]	H									
Juvenile growth (streams)										L-I[3/]							

[1/] At moderate to high water velocities.

[2/] Small effect observed at >4.0 mg/liter, but no higher level tested below the air-saturation level.

[3/] Depending on food availability.

available space and food supplies being limited, and competition for food among excessive numbers of young can even result in depression of production rates. Presumably for these reasons, stocking of natural waters with fry of prolific warmwater fishes has been found usually to have no beneficial effect on fisheries. All these considerations lead to the conclusion that the extent to which non-lethal dissolved oxygen reduction will impair fish production cannot be predicted, or even approximately estimated, on the basis of known effects on sustained swimming speeds or on hatching time and size, or even hatching success, except when reproduction is quite considerably reduced.

Effects of dissolved oxygen reduction on growth rates of fish in the laboratory, especially under simulated natural conditions such as those in our laboratory streams and artificial ponds, seem to offer more promise as a basis for estimates of effects on production rates. The rate of production is directly proportional to growth rate, since it is the mathematical product of biomass and growth rate. And, unexpectedly, we have observed rather close correspondence between effects of reductions of dissolved oxygen on the growth rates of largemouth bass kept on unrestricted rations in laboratory aquaria and their effects on the growth rates of these fish under the much more nearly natural conditions in our artificial ponds, where the rates of growth were far less than the maximal rates attainable in the aquaria. This observation suggests that growth rates under entirely natural conditions may be similarly affected by decreases in oxygen concentration, if the availability of food is not decreased.

We cannot, of course, assert that organic pollution or enrichment of waters will have no effect on the supplies of fish foods; it may bring about either an increase or a decrease in the abundance of suitable food organisms. We also cannot assert that the reproduction of fish will never be seriously impaired by organic pollution and consequent dissolved oxygen reduction that has only a moderate effect on the growth rates of juveniles. But Dudley (1969)* concluded from the results of his experiments that the production of normal larvae of largemouth bass equal to that which occurs at the 90 percent saturation level of dissolved oxygen apparently is possible at levels above 2.0, 2.5 and 3.5 mg/l when incubation temperatures are 15, 20, and 25C, respectively. Thus, the assumption that the reproduction of largemouth bass will not usually be materially impaired by reduction of dissolved oxygen to levels above 3.5 mg/l at normal temperatures appears to be not without justification. Yet reductions of juvenile growth rates of this species in excess of 20 percent from rates observed at concentrations near the air-saturation levels were demonstrable at such reduced concentrations, except in some experiments at low temperatures (Fig. 20).

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*Dudley, R. G. 1969. Survival of largemouth bass embryos at low dissolved oxygen concentrations. M.S. Thesis. Cornell Univ., Ithaca New York. 61p.

If, then, we accept the several necessary assumptions specified above, and take a 20 percent reduction of production rates to be the maximum acceptable degree of impairment (as compared with the production possible at the saturation levels of dissolved oxygen), from the curves in Figure 20 we can arrive at the following provisional estimates of oxygen concentrations above which production of largemouth bass should not be excessively impaired, especially if these minimum concentrations do not persist for very long periods: 2.5, 2.6, 3.7, 3.8, and 4.2 mg/l, at temperatures of 10, 15, 24 and 26, 29, and 20C, respectively. If only 10 percent reduction of production rates from the rates possible at high oxygen concentrations is to be regarded as acceptable, the corresponding estimated dissolved oxygen levels compatible with this degree of impairment of production, according to Figure 20, become: 3.0, 5.5, 5.0, 4.7, 5.1 mg/l at temperatures of 10 and 15, 20, 24, 26, and 29C, respectively.

Coho salmon, whose eggs are buried in gravel, present a more complex problem. Our experiments with this species and other salmonids have shown oxygen concentrations above 3 mg/l to be adequate for successful hatching of alevins and eventual attainment by them of nearly normal size, at high water velocities in the laboratory. Oxygen concentrations in water percolating through streambed gravels, often, however, are far below those to be found in the water flowing over the gravels. Water velocities in these gravels are also usually very low. Thus, reduction of dissolved oxygen in above-gravel stream waters to levels well above demonstrably lethal levels can result in total or almost total destruction of embryos and fry in the gravels. Fish production is not possible, of course, in the absence of successful reproduction.

We may perhaps assume, however, that the most serious reduction of dissolved oxygen concentration in streams inhabited by coho salmon will occur during periods of low stream flow and high temperatures, when coho salmon embryos are not in the gravel, and not during the late fall and winter spawning season. Then, production again can be regarded as being impaired by reduced oxygen concentrations predominantly through their effects on juvenile growth rates. It must be recognized that, since most of the growth of coho salmon occurs during their residence in salt water, success of their reproduction may be a more important factor affecting the yield to fisheries than is the growth rate of the young in the streams, when reproduction is not sufficient to populate the streams to the extent of their holding capacity. Furthermore, since the oxygen concentrations in streambed gravels of some portions of riffle bottoms are very low naturally, any reduction of the oxygen concentration in water flowing over the gravels must result in some restriction of areas suitable for spawning. Thus, the possible effects on reproduction of even moderate reductions of dissolved oxygen

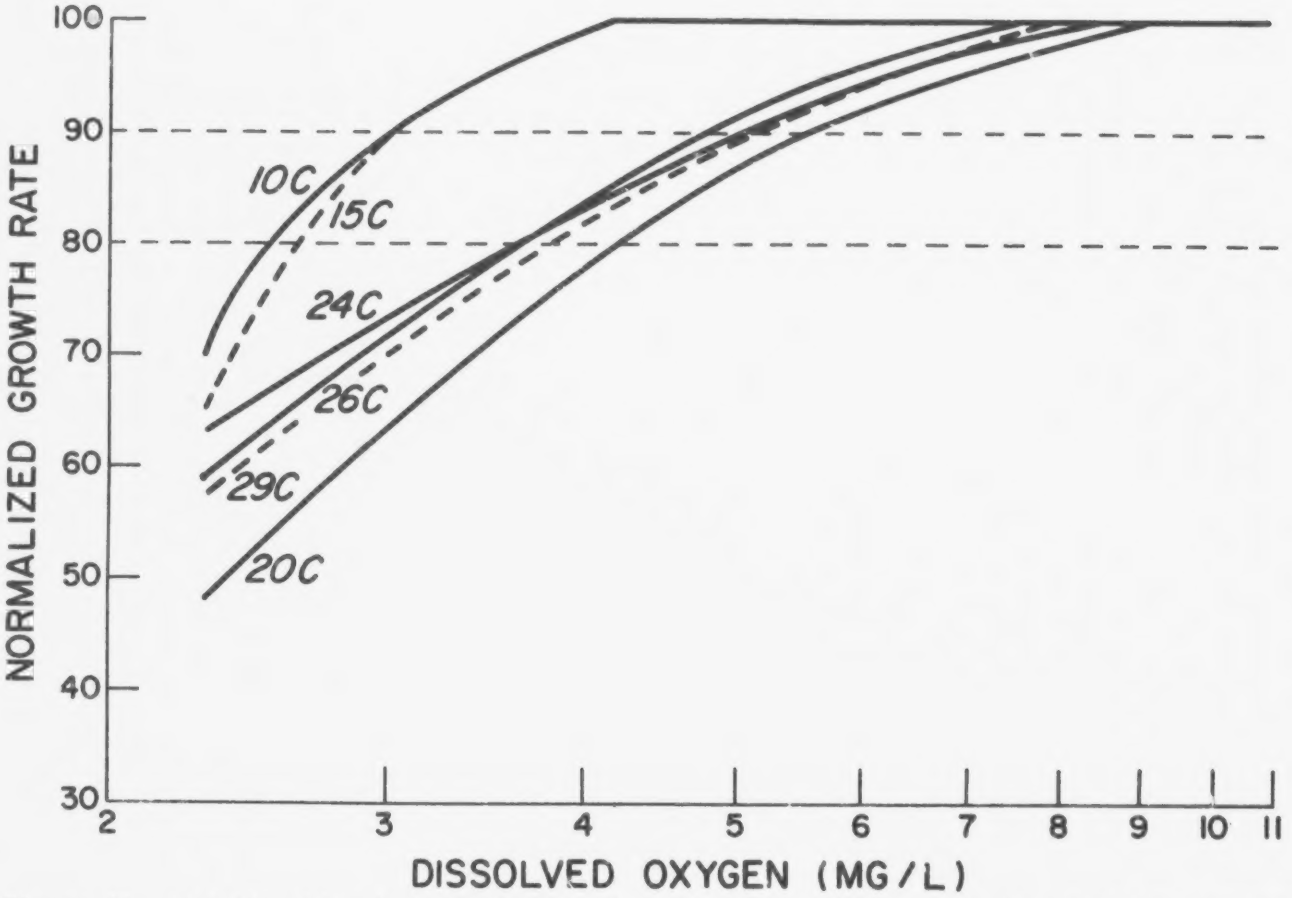

Figure 20. Relationships between dissolved oxygen concentration and the normalized growth rate of juvenile largemouth bass reared in aquaria and fed to repletion on live food at temperatures ranging from 10 to 29C. Growth rates were normalized on the basis that maximum growth occurred at air saturation levels of oxygen.

in streams where coho salmon embryos or larvae are present cannot be disregarded. Still, it seems not unreasonable to suppose, for present purposes, that the dissolved oxygen conditions most critical for coho salmon production in streams will generally occur during periods of low stream flow and high temperature. Then we can estimate, by reference to the curves in Figure 21, as we have done in the case of largemouth bass, that if production is not to be reduced at any time by more than 20 percent from that possible at the air-saturation level of dissolved oxygen, then oxygen concentrations above 4 mg/l must be maintained when temperatures are not much above 20C. If no more than a 10 percent reduction of production rate is to be acceptable at any time, the corresponding lower limit of dissolved oxygen will be near 5 mg/l. These values are based predominantly on the 18-20C curve in Figure 21, which curve represents the combined (averaged) data from a large number of experiments performed at different times by three investigators, whereas the curves for other temperatures represent results of only one or two experiments. The 22C curve (based on two experiments) indicates that, at unusually high temperatures near 22C, the minimum dissolved oxygen requirements for coho salmon production equal to 80 and 90 percent of that possible at high oxygen concentrations may be about 5 mg/l and 5.5 or 6 mg/l, respectively.

In arriving at these estimates, it has been necessary for us to ignore the seemingly aberrant and still unexplained results of some of our experiments, performed in summer or early fall, in which reductions of oxygen concentration to about 4 and 5 mg/l caused reduction of growth rates of coho salmon far exceeding 20 percent and even caused high mortalities of the test animals. Considerations such as this, among many others, led Doudoroff and Shumway (1970) to recommend criteria for a moderate level of protection of freshwater fisheries in general in waters naturally rich in dissolved oxygen that are considerably more conservative than the above criteria based on most of our growth rate data. It should be noted, on the other hand, that the latter criteria are based on the stated limits of depression of growth or production rates from rates observed under nearly ideal conditions at air-saturation levels of dissolved oxygen. Average natural dissolved oxygen levels, especially in habitats of the largemouth bass, are often well below saturation levels. When such is the case, reduction of dissolved oxygen in the natural habitat to the specified minima should not reduce growth and production rates from the natural levels by as much as the percentages indicated by us. Unlike the criteria presented here, which are simple minimum concentration limits, those of Doudoroff and Shumway prescribe acceptable reductions below estimated natural levels (seasonal minima) of dissolved oxygen (See Appendix III).

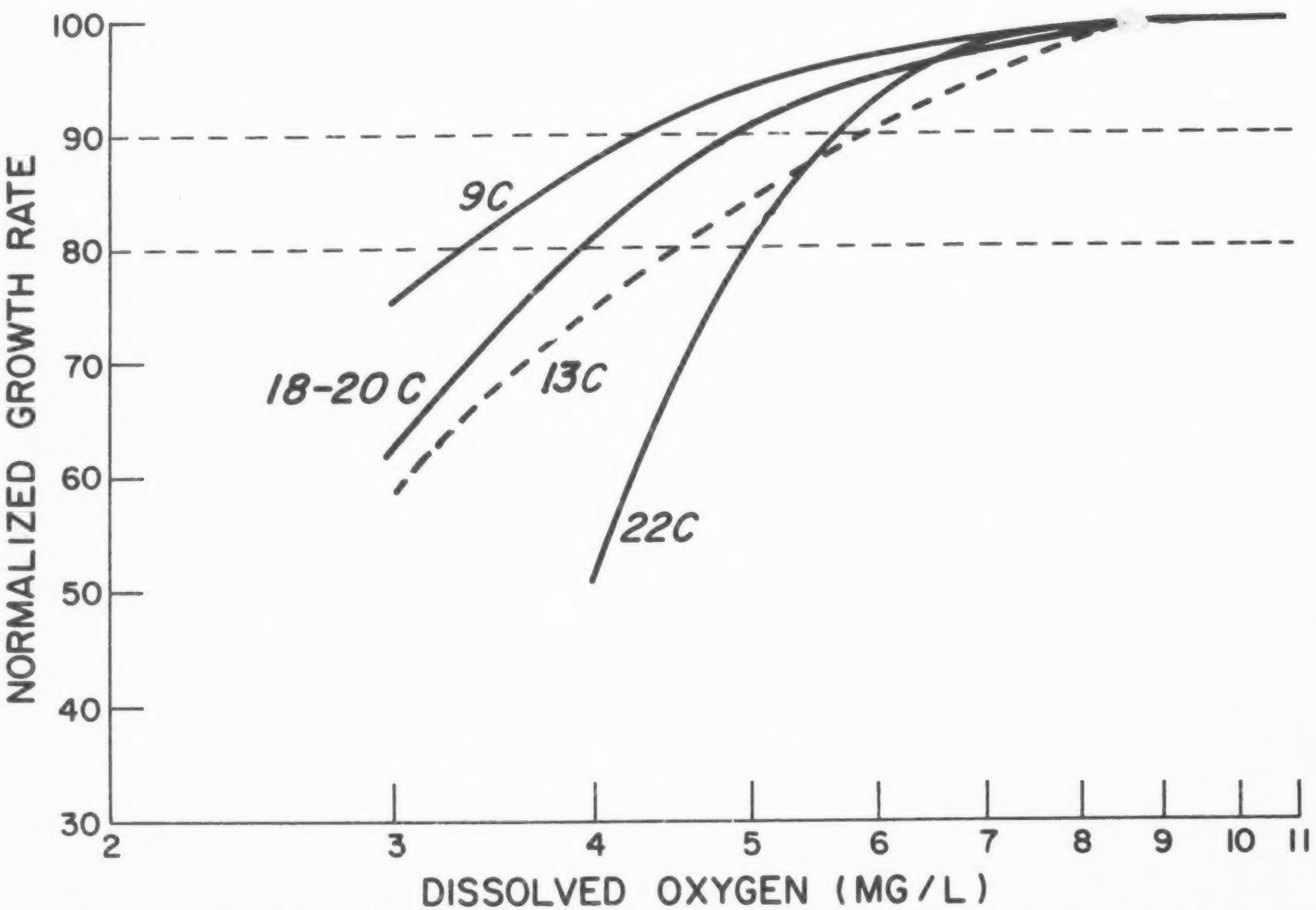

Figure 21. Relationships between dissolved oxygen concentration and the normalized growth rate of juvenile coho salmon reared in aquaria and fed unrestricted rations of live food at temperatures ranging from 9 to 22C. Growth rates were normalized on the basis of determined or estimated growth rates at air saturation levels of oxygen. The 18-20C curve is based on many more experiments than the other curves and is considered to be more reliable.

RECOMMENDATIONS FOR FUTURE RESEARCH ON THE DISSOLVED OXYGEN REQUIREMENTS OF FISHES

LETHAL LEVELS

Mere determination, or redetermination by improved techniques, of lethal thresholds, or lower incipient lethal levels, of dissolved oxygen concentration for adults and juveniles of various fish species no longer appears to be worthwhile, because water quality standards apparently cannot be reasonably based on these lower limits of tolerance. Determinations of tolerance limits could, however, be profitably undertaken for comparative purposes in connection with further studies of *intraspecific* variation of dissolved oxygen requirements, such work heretofore having been reported in the USSR literature only. The extent to which populations of fishes of the same species vary in their dissolved oxygen requirements with variations of dissolved oxygen and other environmental conditions in their native habitats is a matter that appears to be highly pertinent to the establishment of water quality criteria intended for nation-wide application. A question of biological interest and practical importance, apparently not touched upon in the Soviet literature, is the extent to which the intraspecific differences in question are genetic and not due to reversible or irreversible physiological acclimation or adaptation of individual organisms to their environment. Seasonal variations of dissolved oxygen requirements, not yet well understood, also can be profitably investigated through comparative evaluation of lethal levels.

EFFECTS ON REPRODUCTION

The effects of dissolved oxygen on the embryonic development, hatching, and larval growth of the salmonid fishes have been rather extensively studied in the laboratory. Nevertheless, further studies are needed of the relation between size (or stage of development) of salmonid embryos at the time of hatching (as determined by dissolved oxygen conditions during embryonic development) and their subsequent survival until and after successful emergence from gravels under natural or simulated natural conditions. Detailed studies of the direct effects of fine sediments on the survival of embryos and larvae in gravels subject to siltation are also needed. There is considerable evidence that reduction of dissolved oxygen in water percolating through the gravels is not the only cause of observed impairment of survival in silted gravels (Doudoroff and Shumway, 1970).

Much more pressing than the need for more information on the influence of dissolved oxygen on the development of the salmonid fishes is the need for similar information pertaining to various warmwater fishes. There is now a notable dearth of such information. Data in the USSR literature indicating very high dissolved oxygen requirements for successful development and survival of embryos of some warmwater fishes, especially those that normally develop in standing water, need verification. If these requirements are indeed as high as they have been reported to be, water quality standards designed for the protection of important American fishes must be based in very large degree on pertinent information of this kind, which is almost totally lacking in published American literature. Studies of the influence of dissolved oxygen on the fecundity of mature fishes can be profitably undertaken, as can studies of influences on reproductive behavior.

EFFECTS ON GROWTH OF JUVENILE FISHES

Further studies of the influence of dissolved oxygen on food consumption and growth almost certainly are needed. But until close correspondence has been conclusively demonstrated between the effects of dissolved oxygen reductions on growth under nearly natural conditions and their effects on growth under the highly unnatural conditions in laboratory aquaria in which consumption of restricted or unrestricted rations requires virtually no effort on the part of the fish, emphasis on simulation of natural conditions in the experimental work on growth is deemed essential. With facilities already available, we hope to be able to continue some studies on the influence of dissolved oxygen on the growth of predaceous fishes feeding on smaller fish in artificial ponds. Conclusions based on such studies, however, are not necessarily applicable to fishes having very different feeding habits, such as more spontaneously active plankton-eaters and fishes feeding predominantly on drifting organisms in streams. The relation between food availability and dissolved oxygen requirements for unimpaired growth of the different kinds of fishes needs especially to be fully explored. Variations with temperature of the critical levels of dissolved oxygen at which growth begins to be impaired also need further investigation.

EFFECTS ON SWIMMING PERFORMANCE AND ACTIVITY

Probably little more of practical value can be learned through further studies of the influence of dissolved oxygen on the maximum sustained swimming speeds of fishes. Even studies of its effects, if any, on the ecologically more important "burst" swimming speeds of previously resting fish probably would not be highly instructive (Doudoroff and Shumway, 1970). More instructive would be experimental studies of the influence of dissolved oxygen on the feeding activity and success of fishes feeding freely in a natural manner on their typical prey. These studies should be closely associated with the above recommended studies on the effects of oxygen on food consumption and growth rates.

AVOIDANCE REACTIONS

The ability of fishes to respond to horizontal gradients of dissolved oxygen concentration under natural or nearly natural conditions has been neither proved nor disproved by published results of laboratory experiments. Experimental studies of the movements of fishes in oxygen concentration gradients in which the transition from high to low concentrations is very gradual (i.e., occurs over relatively long distances) could be more instructive that the reaction studies reported in the past, and the results would be more applicable to practical problems than the information now available. Additional studies in the field on interference with spawning migrations of fishes, especially salmonids, by reduced oxygen concentrations certainly are needed.

RESPIRATORY AND OXYGEN CONSUMPTION RATES

It is unlikely that much of practical value in connection with the establishment of water quality criteria is to be learned through further studies of the influence of dissolved oxygen on respiratory and oxygen consumption rates of fish confined in the respirometers. This applies also to determination of critical levels of dissolved oxygen for respiratory metabolism, except perhaps under nearly natural conditions (by means of energy-balance methods for estimation of metabolic rates).

FISH POPULATIONS IN NATURAL HABITATS

More field studies of the variety, abundance, and growth rates of fishes in waters subject to organic pollution, in relation to dissolved oxygen concentrations (seasonal minima and averages) that occur in these environments can provide much information of value, even though observed responses of the fish populations may not be responses to reduced oxygen concentrations alone. With modern, continuous-recording, dissolved oxygen meters, much more reliable information of this nature can be obtained than that on which early conclusions and water quality criteria have been based.

RESEARCH PRIORITIES

Assignment of priorities for investigations such as those suggested above involves necessarily a choice of assumptions to be made that bear on the practical significance or relative value of different kinds of information. An appropriate procedure, or logical scheme for research planning, is presented and explained in Appendix II, where the most important alternative assumptions that may be accepted or rejected are presented in a systematic manner. In arriving at the above recommendations for future research, we have tentatively accepted some of these assumptions or propositions, thus rejecting the alternative (antithetical) ones, or we have indicated a preference; but we chose to take no definite position at this time with respect to many others.

APPENDIX I

PUBLICATIONS AND THESES RESULTING FROM THIS PROJECT

PUBLICATIONS

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APPENDIX II

A TENTATIVE LOGICAL SCHEME FOR IDENTIFYING RESEARCH NEEDED FOR THE DEVELOPMENT OF DISSOLVED OXYGEN CRITERIA AND STANDARDS

EXPLANATORY INTRODUCTION

There continues to be a serious need to identify those kinds of research on the dissolved oxygen requirements of fish that will most directly lead to information adequate for setting reliable water quality standards. And, because the information is likely to continue to be more or less inadequate, there is a need to identify the real weaknesses in the information, so that as we necessarily set standards we are well aware of just how they are likely to be unreliable.

Biologists knowledgeable about the water quality requirements of fish have often been hesitant to advance firm recommendations as to water quality standards for the protection of these fish. Considering the complexity of factors and responses involved in determining the oxygen needs of fish, and the inadequacy of knowledge, such hesitancy is understandable. But the social need to make use of such knowledge as we may have, the complexity of natural systems, and the inadequacy of existing knowledge are not peculiar to biology as a science or to present times. Any use of or advance in knowledge is based on a system of assumptions, known and unknown, stated and unstated. The physical sciences have advanced more rapidly than the biological sciences, and advances have been more expediently applied, in very large part because of formal recognition of the assumptions underlying any system of thought or application. Given certain assumptions or propositions, we can deductively arrive at valid conclusions. If the assumptions do not correctly represent reality, our conclusions, even if logically valid, may not be true.

But such a deductive system in which conclusions are clearly tied to specified assumptions permits the scientist to make scientific judgments and the administrator to make social judgments, according to how they want to weight the risks involved in the assumptions. If the risks are too great, more research is necessary, and the nature of that research is identified.

Much of the disagreement over the research necessary to set water quality standards and over just how the research should be interpretated in setting standards has been trivial or semantic, even when very knowledgeable people have been involved, because of failure to specify the assumptions on which any line of reasoning or argument is based. We have here attempted to develop a logical scheme for identifying research necessary for setting dissolved oxygen standards for fish. Development of such a scheme is not an easy thing to do. Nor is reading with understanding such a scheme. But both are preferable to years of poorly conceived research, failure of biologists to make clear recommendation based on identified assumptions, or poor application of knowledge in the setting of standards. We believe that general development of such schemes in water pollution research and control would be a very great step ahead.

The scheme that we have developed is based on the assumption that it is a product of interest to be protected, not that the biological community is to be protected against any change whatsoever. Furthermore, this scheme is based on the assumption that it is the production of the product of interest--its total tissue elaboration (relative growth rate x biomass)--that is most important and is to be protected. Reproduction, behavior, and other biological responses, then, become important only insofar as they influence production. The scheme as developed is only sufficiently complex to suggest the research necessary to determine water quality standards that would be adequate to prevent any considerable level of impairment of fish production. If other levels of protection are to be considered, then not only the logical scheme but also the research necessary must become more complex.

In general, two kinds of assumptions or propositions, regulatory and biological, have been used in developing this logical scheme. The necessary assumptions may have to do with the nature or manner of application of the criteria, with the importance of various other environmental factors that may influence the oxygen requirements, with the relative sensitivity of different life-history stages or of different ecologically important physiological functions of fish to oxygen deficiency (i.e., their relative susceptibility to injury), and so forth. The present scheme represents an attempt to identify the more important assumptions that sometimes have been or may possibly be made, and to present them in a systematic fashion, together with conclusions to which they are believed to lead concerning the nature of needed investigations.

The logical scheme here presented consists of a series of pairs of antithetical propositions or assumptions. These are designated by arabic numerals or combinations of these and the letter A. The letter A at the end of a numerical designation signifies that the proposition or assumption so designated is the antithesis of the preceding proposition or assumption. For example, Proposition 1A is the antithesis of Prop. 1; Prop. 8.1A is the antithesis of Prop. 8.1; and Prop. 10A.1A is the antithesis of Prop. 10A.1. One or the other or neither of the two propositions or assumptions of each pair may be rejected. If only one proposition of each pair is accepted and the other is rejected, use of this scheme will lead (with only one exception) to but a single final conclusion concerning the nature of needed investigations. Whenever, because of inadequacy of available information and consequent uncertainty, neither proposition of a pair is rejected, more than one final conclusion usually will be reached, this result indicating that more than one kind of study is needed. The different conclusions are designated by roman numerals. Some of the conclusions so designated (Conclusions I, II, III, IV, and V) are not final conclusions. They are "modifying conclusions" indicating that the conclusion or conclusions finally reached by proceeding with the use of the scheme (i.e., going to the next appropriate pair of antithetical propositions according to directions given) must be modified in the specified manner. Each modifying conclusion and each proposition that does not immediately lead to a conclusion is followed by a notation directing the reader to the next appropriate proposition to be considered.

Some of the stated propositions are deemed certainly untenable, but all are presented impartially, no preference for acceptance or rejection of any proposition being indicated. It should be understood, however, that innumerable assumptions other than those listed had to be made in devising this scheme. We must and can safely assume, for example, that the condition of the stock market or the national economy has no influence on the oxygen requirements of fishes. The validity of some other assumptions that have been made is not as incontestable as the validity of the foregoing assumptions. For example, on the basis of available information, we have assumed that hydrostatic pressure has no important influence on the dissolved oxygen requirements of fish, or no significant bearing on dissolved oxygen criteria designed for their protection. This assumption and its antithesis could have been included in the listed series of assumptions, but the inclusion of all such assumptions would have rendered the list too long and the scheme too involved.

For the sake of simplicity, many pertinent considerations, such as possible or known influences on the dissolved oxygen requirements of size and age of fish, of season of the year, of the velocity of water around developing fish embryos, etc., have been largely or entirely disregarded. Also not specifically considered is the bearing on the design of water quality criteria of the sometimes wide diurnal fluctuations in dissolved oxygen in fish habitats, and of the large differences between dissolved oxygen levels to which fish embryos are exposed that are buried deep in streambed gravels (e.g., salmonid embryos) and the dissolved oxygen concentrations in the waters flowing over the gravels. It is assumed, instead, that all of these matters will be given proper consideration in the design of the experimental or other investigations recommended in the "conclusions," to the extent that they appear to be pertinent. Further elaboration of the proposed logical scheme doubtless would have made possible the inclusion and full consideration of all these matters, but the present scheme is tentative and is deemed sufficiently involved. Present knowledge of the dissolved oxygen (DO) requirements of fishes and of factors influencing these requirements being still very limited, it is clearly impossible to delimit the scope of needed further investigations very precisely or narrowly.

THE TENTATIVE LOGICAL SCHEME

1. Concentrations of toxic pollutants are to be limited to levels not harmful at approved DO levels: Concentrations of toxic substances in waters receiving wastes are to be regulated so as to have no seriously adverse effect on fish production as long as acceptable DO levels are maintained (i.e., levels not below prescribed minima based on requirements of fishes in the absence of these substances). See Prop. 2.

1A. Concentrations of toxicants are not to be so limited, and thus DO criteria must vary with the kind and degree of toxic pollution. See Conclusion I.

> Conclusion I. *DO requirements of fishes must be determined in the presence of every possible combination of toxic pollutants and at widely varying levels of pollution with each of these toxicants and combinations of toxicants (or at least at the highestlevel that may occur, if such maxima can be predicted or are to be prescribed). The following additional alternatives can then be used to determine the kinds of studies required for evaluating a minimum DO level that is harmless or acceptable under each of these possible conditions.* See Prop. 2.

2. Ordinary variations of water quality, except temperature, need not be considered in establishing DO criteria: Variations of the dissolved mineral and gas content, other than DO content, of water receiving oxygen-demanding organic wastes--including variations of free carbon dioxide content and pH within the limits of usual variation--do not materially influence the DO requirements of fishes. See Prop. 3.

2A. Ordinary variations of water quality cannot be neglected. See Conclusion II.

> Conclusion II. *The dissolved oxygen requirements of fish must be determined under widely varying conditions of dissolved mineral and gas content of their medium, or, if the same criteria are to be applied to all waters, under the most adverse conditions likely to be encountered. The following additional alternatives can then be used for determining what studies are needed to arrive at the minimum DO levels that are harmless under the different conditions or under the most adverse conditions.* See Prop. 3.

3. Prescribed DO concentrations are not to vary with water temperature: DO concentrations are to be maintained at levels harmless to fish and their embryos at the maximum temperatures to which they or their embryos may be subjected. See Prop. 4.

3A. DO criteria are to vary with the water temperature.

> Conclusion III. *The DO requirements of fishes must be determined at different temperatures varying over the entire range of temperatures likely to occur in the natural habitats of the fish. The following additional alternatives can then be used for determining what studies are needed to arrive at the minimum DO level that is harmless at each of a series of selected temperatures, rather than at the maximum temperature.* See Prop. 4.

4. DO criteria are to be prescribed for large classes of fish habitats or fish faunas, and not for individual fish species: Acceptable DO levels can and are to be based on requirements for essentially unimpaired production of one or a few selected, important fish species believed to be relatively sensitive to DO deficiency and adequately representative of species to be protected in all fish habitats of a given kind or class (e.g., all cold waters in which salmonid fishes are of outstanding importance). See Prop. 5.

4A. DO criteria are to be prescribed for particular species of fish to be protected. See. Prop. 4A.1.

4A.1. Possible genetic adaptation and racial differences can be neglected. The possibility of considerable genetic adaptation (i.e., adaptive alteration of genotypes through natural selection) and consequent intraspecific differences of fish populations can be disregarded in evaluating the DO requirement of a fish species. See Conclusion IV.

> Conclusion IV: *DO requirements must be determined for a representative population of each fish species of interest. The following additional alternatives can then be used for determining what studies are needed to arrive at the minimum DO level that is harmless or suitable for a given species.* See Prop. 5.

4A.1A. The possibility of genetic adaptation can not be disregarded. See Conclusion V:

> Conclusion V: *DO requirements must be evaluated for a population of each species of interest that has been adapted through several generations to oxygen-deficient water that is tolerable but clearly unfavorable for a nonadapted population. The following additional alternatives can then be used for determining what studies are needed to arrive at minimum DO levels that are harmless or suitable for the adapted populations of the species of interest.* See Prop. 5.

5. Non-lethal DO levels harmful to fish production will not persist where rapidly lethal levels are prevented: In waters receiving organic wastes, DO levels near or below levels that are lethal for juvenile and adult fish will persist for short periods only, such as (a) 6 hours, (b) 24 hours, or (3) 4 days; and if the depression of DO to lethal levels is prevented at all times, adequate DO levels generally will prevail, so that fish production will not be materially impaired. See Conclusion VI.

> Conclusion VI: *Only the more or less rapidly lethal levels need to be determined for the selected, representative fish species[1] at the maximum temperatures likely to occur in their natural habitats when DO levels are low.[2]*
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>
> [1] *Or all species of interest if Prop. 4 is rejected. Suitably genetically adapted stocks of these fish must be used if Prop. 4A.1 also is rejected.*
>
> [2] *Or at a series of widely different temperatures, if Prop. 3 is rejected.*

5A. Prevention of lethal levels is insufficient to ensure unimpaired fish production. See Prop. 6.

6. Fish are not found in nature at unfavorable DO levels that can be avoided: By reacting appropriately to low DO or associated increased CO_2 levels, fish almost invariably avoid in nature DO levels detrimental to their production unless they are trapped in waters having such low DO content. See Conclusion VII.

> Conclusion VII: *Only field studies of fish distribution or movements in relation to DO need to be undertaken, determining minimum DO levels at which selected, representative species of fish[1] occur naturally, and which they apparently could have avoided, at maximum habitat temperatures.[2]*

6 A. Fish will not always avoid in nature DO levels inimical to their production. See Prop. 7.

7. Avoidance of unfavorable DO levels, and of those levels only, in laboratory tests will occur: Under appropriate laboratory conditions, fish will always markedly avoid DO levels that are inimical for their production under natural conditions, even though they may be unable to do so in nature (where gradients are not as steep or regular), but they will not avoid harmless concentrations. See Conclusion VIII.

> Conclusion VIII. *Only DO levels that are avoided by selected representative fish* [1] *in appropriate laboratory tests at maximum habitat temperatures*[2] *need to be determined.*

7 .A. Avoidance reactions in laboratory tests may not indicate limits of favorable DO concentration. See Prop. 8.

8. Effects of reduced DO on the swimming performance and behavior of fish are of primary importance: The swimming ability of fish or their behavior is affected materially, so that production under natural conditions is reduced (because of increased susceptibility of the fish to predation, etc.) at DO levels above those at which harmful effects on reproduction or growth are clearly demonstrable. See Conclusion IX.

> Conclusion IX: *Laboratory studies of the influence of DO on the swimming ability (both "sustained" and "burst" swimming performance) or the behavior of selected, representative fish species*[1]*, at nearly the highest temperatures occurring in their environments*[2]*, are needed.*

8 .A. Effects of reduced DO on swimming ability and behavior of fish at DO levels favorable for their reproduction and growth are immaterial. See Prop. 9.

9. Effects of reduced DO on reproduction are important: At DO levels that have any depressing effect (direct or indirect) on growth, the impairment of reproduction is pronounced and sufficient to have a significant depressing effect on production. See Prop. 9.1.

9 .A. Reduced DO levels at which reproduction is materially impaired are below those at which growth begins to be affected. See Prop. 10.

9.1. Lowest DO levels in the waters under consideration are likely to occur where spawning normally takes place and during the reproductive season. See Prop. 9.2.

9.1.A. DO minima occurring during the reproductive season and where spawning normally takes place are well above levels that occur at other times or elsewhere in the normal habitats of the fish. See Conclusion X.

Conclusion X: *Studies of the influence of DO on both growth and reproduction (fecundity or early development) are needed. The following additional alternatives can be used for determining the nature of needed studies of both kinds.* See both Prop. 9.2 and Prop. 10.

9.2. Unimpaired fecundity in the laboratory indicates DO levels sufficient for adequate reproduction in nature: Reduced DO levels at which the fecundity of fish is not materially reduced in the laboratory are adequate also for adequate reproduction under natural conditions (i.e., reproduction sufficient for unimpaired production). See Conclusion XI.

Conclusion XI: *Laboratory studies are needed of the influence of DO on the fecundity and spawning of selected, representative fish species*[1] *at maximum temperatures likely to occur in their environment during the reproductive season.*[2]

9.2.A. Lowest DO levels at which fecundity is not reduced materially in laboratory tests are less than those necessary for virtually unimpaired reproduction in nature. See Prop. 9.3.

9.3. Unimpaired laboratory hatching success and survival of young indicate DO levels suitable for adequate reproduction in nature: Reduced DO levels at which the percentage of successful hatching of fish eggs and survival of young fry in the laboratory under appropriate test conditions are not materially reduced are adequate for adequate reproduction under natural conditions (i.e., reproduction sufficient for unimpaired production). See Conclusion XII.

Conclusion XII. *Laboratory determination is needed of DO levels at which the hatching success of selected, representative fish species*[1] *begins to be materially impaired under the most unfavorable water velocity and temperature conditions to which their embryos and larvae are likely to be frequently exposed in nature (i.e., at relatively low water velocities and at temperatures relatively high for the reproductive season).*[2]

9.3.A. Lowest DO levels at which hatching success and survival of young fry are not materially reduced in simple laboratory tests are less than those necessary for adequate natural reproduction. See Prop. 9.4.

9.4. Hatching size and time in laboratory tests indicate DO levels required for adequate reproduction in nature: Reduced DO levels at which the size and degree of development of hatching larvae are appreciably reduced or hatching is measurably delayed under appropriate test conditions in an unnatural laboratory will result in materially impaired reproduction (i.e., production of young and their survival to the juvenile stage) under natural conditions, whereas higher DO levels will not, there being no material impairment of fecundity, reproductive behavior, or viability of the larvae at the higher levels. See Conclusion XIII.

> Conclusion XIII. *Laboratory studies of the influence of DO on hatching time and size of selected, representative species of fish*[1] *at the lowest water velocities and highest temperatures to which their embryos are likely to be frequently exposed in nature*[2] *are needed.*

9.4.A. Reduced DO levels below which hatching size of larvae is reduced or hatching is delayed are not reliable and useful indices of DO concentrations necessary for adequate reproduction in nature. See Prop. 9.5.

9.5. DO requirements for adequate natural reproduction can be determined experimentally under more or less natural conditions: The influence of DO on reproduction (i.e., spawning, production of young, and survival through early developmental stages) in nature is reliably determinable through controlled experiments performed under simulated natural conditions in the laboratory or nearly natural conditions in the field. See Conclusion XIV.

> Conclusion XIV: *Studies of the effects of reduced DO on the reproduction of selected, representative fish species*[1] *under simulated natural conditions in the laboratory or nearly natural conditions in the field and at lowest water velocities and highest temperatures to which embryos and larvae are likely to be exposed frequently in nature*[2] *are needed.*

9.5.A. The influence of DO on reproduction in nature cannot be reliably determined experimentally. See Conclusion XV.

> Conclusion XV : *The DO requirements of fish must be inferred from observations on reproduction of selected, representative fish species*[1] *(abundance of young, etc.) under varying, uncontrolled conditions in natural habitats.*

10. Fish are at least as sensitive to organic pollution as their food resources: Reduction of DO by oxygen-depleting organic wastes reduces the food supply of fish only at levels at which exploitation by the fish of normally available food resources is materially impaired. See Prop. 11.

10.A. The food supply of fish is considerably reduced at reduced DO levels having no material direct effect on the feeding and growth of the fish. See Prop. 10A.1.

10.A.1. Effects of organic pollutants on the food resources of fish are uniformly related to their effects on DO levels: Although putrescible organic pollutants have variable nutritive properties, contributing directly or indirectly to the production of some fish food, the effect on the abundance of fish food of organic pollution having a given effect on DO levels is reliably predictable on the basis of knowledge only of the DO requirements of representative fish-food organisms. See Conclusion XVI.

> Conclusion XVI: *Studies of the DO requirements of fish-food organisms and their foods are needed. The proposed scheme pertaining to investigation of the DO requirements of fishes can be used, with some modifications, for determining also the nature of needed laboratory studies on the fish-food organisms.*

10A.1A. Even when effects on DO levels are known, the effects of "organic enrichment" of waters on the food supply of fish cannot be reliably predicted on the basis of knowledge of the DO requirements of representative fish-food species, the relation between DO depression and reduction of food resources being highly variable. See Conclusion XVII.

> Conclusion XVII: *Studies of the effects of varying degrees of contamination of water with different putrescible organic wastes on various complex aquatic communities and on the production of fish foods under otherwise nearly or entirely natural conditions are essential.*

11. Reduction of the metabolic "scope for activity" of fish indicates growth impairment: Any reduction of the maximum, active oxygen uptake (metabolic) rate of a fish and its "scope for activity" (difference between the active and resting rates), or reduction of the scope by some definite fraction (e.g., by one-half) but not by a lesser amount, due to depression of DO will result in material reduction of the food consumption and growth, if not the length of life, of the fish in nature. See Conclusion XVIII.

Conclusion XVIII: *Studies of the influence of DO on the active oxygen uptake of selected representative fish species*[1/] *in suitable respirometers and on their scope for activity at maximum habitat temperatures*[2/] *are needed.*

11.A. The restriction of the food consumption and growth rates of fish by reduction of DO is not simply related to the restriction of their active oxygen uptake rate or their scope for activity. See Prop. 12.

12. Food abundance is usually the factor limiting food consumption and growth of fish in nature. See Prop. 12.1.

12.A. Food in nature is usually so abundant that its availability is not a factor limiting food consumption and growth of fish under natural conditions. See Conclusion XIX.

Conclusion XIX: *Laboratory aquarium tests in which selected representative fish species*[1/] *are fed unrestricted food rations to determine critical DO levels below which appetite and growth are markedly impaired at maximum habitat temperatures*[2/] *are needed and adequate.*

12.1. Reduced DO levels at which the food intake and growth begin to be markedly restricted (oxygen-dependent) in laboratory aquaria and under natural conditions are nearly the same.

Conclusion: *See Conclusion XIX above, under Prop. 12.A. Acceptance of Prop. 12.1 leads to the same conclusion.*

12.1.A. Critical DO levels below which food consumption and growth rates of fish will be restricted in nature cannot be predicted from results of laboratory experiments in which fish are fed unrestricted food rations in simple aquaria. See Conclusion XX.

Conclusion XX: *Effects of DO reduction on the food consumption and growth of selected, representative fish species*[1/] *at maximum habitat temperatures*[2/] *and different levels of food availability under simulated natural conditions must be determined. Food density and intake rate can be controlled by artificial stocking of the environment or by varying fish biomass levels in environments in which food is produced naturally (e.g., in laboratory streams). The DO requirements for unimpaired growth of the fish will depend on the food availability and consequently will tend to vary with the growth rates of the fish;*

however, the maximum natural food availability, rather than the average availability, in a given fish habitat may be the factor determining the critical DO level for that habitat, if the periods of highest food availability and of seriously reduced DO coincide.

APPENDIX III
ONE POSSIBLE APPROACH TO THE FORMULATION OF DISSOLVED OXYGEN CRITERIA AND STANDARDS FOR THE PROTECTION OF FISHERIES RESOURCES

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Pages 255-275 from
Doudoroff, P., and D. L. Shumway. 1970.
Dissolved Oxygen Requirements of Freshwater
Fishes. Food and Agricultural Organization
of the United Nations. FAO Fisheries
Technical Paper No. 86. 291 p.

SOME CONSIDERATIONS BASIC TO THE FORMULATION OF CRITERIA OR STANDARDS

The difference between the air-saturation level of O_2 and 50% of the air-saturation level may appear to be a large difference, amounting to about 4 to 7 mg/l at ordinary water temperatures. When viewed from a physiological standpoint, however, it is seen not to be actually a very large difference. The logarithmic scale is generally, and with very good reason, accepted as being biologically the most appropriate scale to use in considering differences of concentration or of exposure time. On this scale, the range between 100% and 50% of saturation represents only a modest fraction (less than a quarter) of the total range of O_2 levels to which fish are sometimes exposed in nature and that most fish are able to tolerate at moderate temperatures. It is less than one half of the portion of the tolerable range that lies below the air-saturation level even at ordinary summer temperatures, and a smaller fraction at winter temperatures. When considered in this light, O_2 concentration differences of 1 mg/l within the range of concentrations above 50% of air-saturation are seen to be quite small. This can account for inability of biologists definitely to decide, for example, whether some adverse effect on fish of reduction of O_2 begins at a concentration of 6 mg/l or at 5 mg/l. Any serious disputation concerning such a question would be hairsplitting from a biological standpoint. Even the difference between 7 mg/l and 5 mg/l is not a large difference and its ecological importance consequently may not be readily demonstrable.

Yet, the cost to industry and municipalities of improving waste treatment so as to raise O_2 concentrations in receiving waters by only an extra 1 mg/l would amount to untold millions of dollars. The conscientious and well-informed biologist who is charged with recommending water quality criteria or standards for the protection of fisheries thus is faced with a dilemma. He can see that any large reduction of O_2 below natural levels may prove detrimental to fish production in some waters that support fisheries of immense value. He must not yield to pressure from those who would destroy valuable natural resources for profit or advancement of other personal ends. Yet, having thought deeply upon the problem, he knows also that he cannot honestly assert that the difference between O_2 levels clearly harmful and harmless for fish is as small as 1 mg/l. How, then, can he insist on a particular O_2 level as a minimum acceptable level for all waters that support fish life of some value when faced with the argument that a level only 1 or 2 mg/l lower could be maintained at much less cost to the public? Ultimately, it is the public that must bear the cost of all waste treatment, and this is a fact that a biologist who is a public servant should not forget.

For the biologist's dilemma there is a solution, we suggest, and that solution lies in the adoption of a sound philosophy and system of water quality regulation properly attuned to socio-economic realities. The difficulty with which we are here concerned stems, perhaps, from wide acceptance of the scientifically indefensible proposition that thin lines can be drawn that separate water quality alterations that are virtually harmless to aquatic life from those that are decidedly harmful and therefore unacceptable to an enlightened society. Actually, there are no such lines, but only broad zones of gradual transition from quite unimpaired productivity of waters to total destruction of populations of all valuable aquatic organisms. In the case of dissolved O_2 concentration, we have seen that the zone in question may extend all the way from quite undiminished, natural levels of O_2 to a level as low as 2 mg/l or less. Within such a broad zone, a limit or limits must be defined for administrative purposes. However, such a limit cannot be based on biological judgments alone; social and economic considerations must somehow enter into its determination.

Some waters support or are capable of supporting fisheries of great commercial or recreational value. This value can be easily destroyed by a single improperly located or carelessly designed industrial enterprise of relatively small value to society. But even the slightest risk of serious impairment of a very valuable fishery should be unacceptable to society if it can be avoided at a small cost, a cost that is but a fraction of the possible loss. On the other hand, there are, in densely populated and highly industrialized regions, some naturally unproductive waters supporting fisheries that are and always were of minor importance, because of natural characteristics of the habitats. A high level of protection of these minor fisheries is usually attainable only at a cost to society far in excess of any possible benefits. There are also many waters of intermediate status, whose moderately valuable fishery resources can be given a corresponding, moderate level of protection at a reasonable cost to society. The productivity of these waters can usually be maintained at a high level, but some impairment or risk of impairment of this productivity unfortunately must be accepted as an unavoidable accompaniment of growth of population and industry.

The sooner we squarely face the fact that we are concerned not with a choice between protecting and not protecting fisheries--between white and black--but with a choice of appropriate levels of protection, the sooner will rapid progress be made in the development of sound water quality criteria and standards for the protection of fisheries. This recognition involves the establishment of an appropriate formal or informal system of "use classification" of waters. Use classification of waters can be defined as any administrative classification done with the avowed intention that all waters assigned to a given class shall be maintained in, or returned to, a condition suitable for the same beneficial use or uses through the enforcement of appropriate water quality standards. Various formal systems of use classification of waters are now in use. We have yet to find, however, one that clearly and unequivocally acknowledges the need for different levels of protection of each use, to be determined independently of the levels of protection of any other approved uses of the same waters. Therefore, the need also for different criteria or standards of water quality, appropriate to the different levels of protection of fisheries or other beneficial uses of water, seems not to have been acknowledged. This lack of recognition of the need for more than one level of protection of fisheries, and of most other uses of water too, seems to be reflected in most of the existing water quality standards and criteria of a formal nature.

Criteria of suitability of water for different uses differ widely, and the use that has the highest water quality requirement (with respect to a given measure of water quality) when protection is maximal is not necessarily the most important use of a given water. The requirements of fish life have little relation to those of domestic or agricultural uses of water, for example. Only aquatic life needs much dissolved O_2. Fisheries can be very important and can require the highest degree of protection where domestic and agricultural uses of water are of minor importance and require protection of a lower order. Elsewhere they can be relatively unimportant and require less protection than do the other uses mentioned. Existing classification systems generally are too rigid to provide for protection of each use commensurate with its relative importance locally, and therefore most appropriate to local needs.

As we have indicated already, use classification of waters, formal or informal, must be based on socio-economic considerations--on public desires and willingness to bear--directly or indirectly, the costs of satisfying these desires. Once the objectives of waste treatment or other pollution control measures have thus been adequately defined, science perhaps will be able to go to work more effectively in providing suitable criteria of water quality that are founded on the best available technical information and judgment.

Another important consideration is the biological fact that fish faunas that are to be found in natural, unpolluted waters and the production rates of these fishes of value to man vary widely with the highly variable natural quality of these waters. The degree of impairment of fish production that will result from reduction of the O_2 content of water to some uniform level cannot be independent of the water's natural O_2 content. It should be obvious that no fish species will thrive in any water whose natural O_2 content is intolerable or only barely tolerable for it. Therefore, the abundant species whose production must be protected in a naturally O_2-deficient water will be species that have O_2 requirements quite different from those of some of the valuable species that may need protection in waters naturally rich in O_2. Large differences in O_2 requirements even between populations of fishes of the same species found in, or acclimatized to, naturally very different waters have been reported, and these may have, at least in part, a genetic basis. Living organisms have widely different environmental requirements because they are adapted for life in different natural environments; the variety of these requirements and environments is the principal reason for the variety of biological communities.

Yet, apparently for the sake of engineering and administrative simplicity, these well-known biological truths have been too often overlooked in the formulation of criteria and standards of water quality designed for the protection of aquatic life. In a sincere effort to accommodate engineers and administrators in the field of water pollution control, and doubtless with some misgivings, biologists have for years been willing to assert, for example, that warmwater fish populations or faunas require some minimal O_2 concentration, or a pH within some stated range. Such a criterion clearly implies that all warmwater fish populations or faunas of unpolluted waters are much alike and have essentially the same requirements for their preservation. Yet, we are sure that few biologists would be willing to defend such a thesis.

It is important to note that the variety of environmental requirements of fish faunas has not been usually disregarded, or at least is not now being disregarded, in regulating thermal pollution. The National Technical Advisory Committee on Water Quality Criteria (U.S.A.) stated, for example, in its recent report (Federal Water Pollution Control Administration, 1968) that "no single temperature requirement can be applied to the United States as a whole, or even to one State; the requirements must be closely related to each body of water and its population." These noteworthy additional comments follow: "To do this a temperature increment based on the natural water temperature is more appropriate than an unvarying number. Using an increment requires, however, that we have information on the natural temperature conditions of the water in question...."

One can only wonder why the same principle that was so firmly stated in connection with recommended temperature criteria was not considered pertinent to dissolved O_2 criteria, and also to criteria or recommendations pertaining to alterations of the pH and the turbidity of fresh waters. Interestingly, a recommendation against introduction into coastal waters of materials "that extend the normal ranges of pH at any location by more that ±0.1 pH unit" is included in the section of the committee's report that deals with marine and estuarine organisms. For fresh waters, however, only upper and lower limits (pH 6.0 and 9.0) are recommended; these are well within the range of extreme natural variation. Presumably, any naturally more acid or more alkaline waters should not be rendered still more acid or alkaline even in small degree, according to these recommendation.

The committee's recommendations are not fundamentally very different from long-established practice. But it is this long-established practice that we here propose to reject in favor of one that we believe to be more easily defensible biologically. Without such a departure from precedents, we feel that we could contribute little of practical value, certainly no very solid recommendations, on the basis of our detailed study of background information.

RECOMMENDED CRITERIA AND THEIR APPLICATION

As we have already indicated, the criteria that we are recommending here differ in two important respects from those now widely used. Firstly, they are not fixed values independent of natural conditions. Secondly, by offering a choice, they provide for several different levels of protection of fisheries, the selection of any one of which would be primarily a socio-economic decision, not a biological one.

The criteria can best be presented graphically (Figure 1). Their formulation admittedly required much exercise of personal judgment, and they may therefore be deemed arbitrary. However, they do derive from conclusions to which our own research and our detailed study of the results of other research that are reviewed in this treatise have led us. We think that they are probably somewhat more accordant with pertinent biological principles and results of recent research than are other comparable criteria pertaining to dissolved O_2 now used in connection with water pollution control.

Each line or curve in Figure 1 depicts the relation between estimated natural O_2 concentration minima in fresh waters for any given season of the year and the seasonal minima that we judge compatible with a specified level of protection of fisheries in the same waters. In other words, each shows the level to which we suppose the dissolved O_2 can be depressed below the estimated natural minimum for the same season of the year while still providing the stated level of protection for local fisheries. The five lines or curves thus are supposed to represent, or to be appropriate to, different levels of protection of fisheries. One of these levels or another may be selected on the basis of socio-economic considerations, in classifying a water according to its intended best uses.

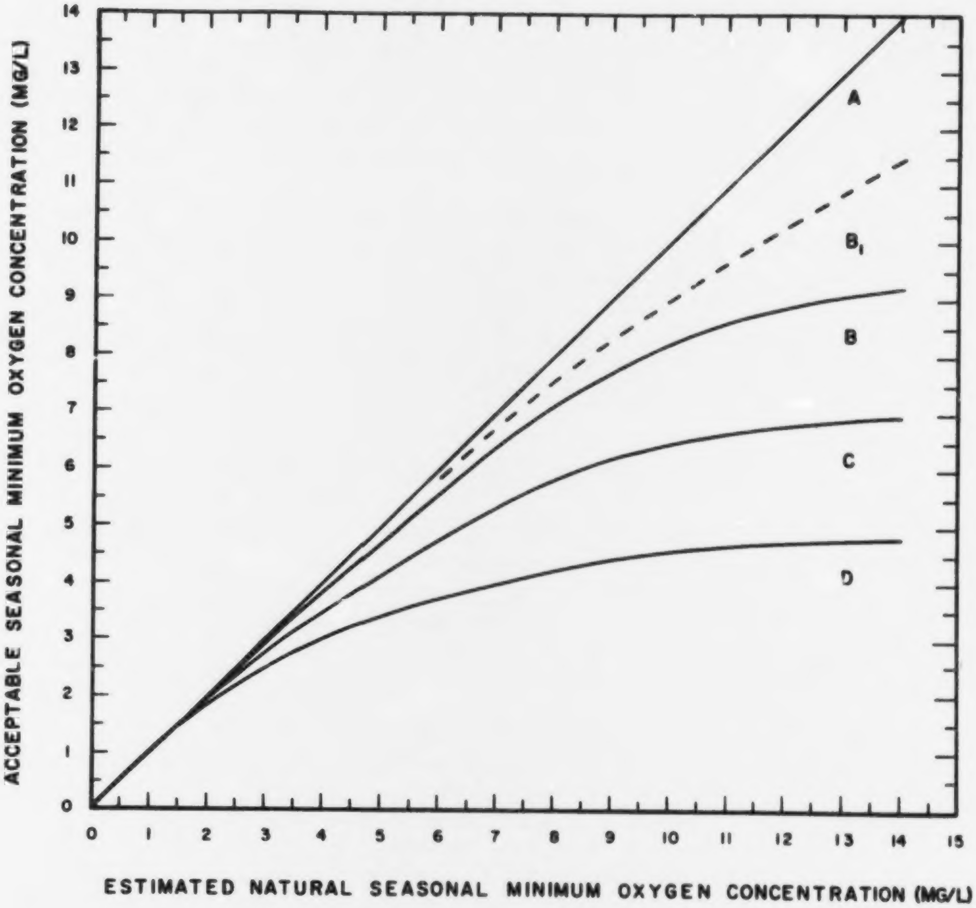


Figure 1. Proposed dissolved oxygen criteria for protection of freshwater fisheries: Curves relating "acceptable" seasonal dissolved oxygen minima, or minimum levels that are deemed appropriate to different, specified levels of protection of fisheries, to estimated natural seasonal minima. Curves or lines designated A, B_1, B, C, and D correspond to levels of protection described in the text.

As used here, the word "season" means a period, defined with attention to local climatic and hydrologic conditions, during which the natural thermal and dissolved O_2 regime of a stream or lake can be expected to be fairly uniform. Usually, division of the year into four equal (3-month) periods, such as December-February (winter), March-May (spring), June-August (summer), and September-November (fall) probably will be satisfactory. However, under special conditions, the designated "seasons" can be periods longer or shorter than three months; they need not necessarily be equal in length.

The oblique, straight line designated A in Figure 1 represents no depression of the O_2 concentration in any season of the year below the estimated natural minimum level for the same season. Thus, it represents nearly maximal protection of fishery resources. Protection at this high level can be appropriate for some prime spawning grounds on which major fisheries are dependent in large measure, and it will almost fully ensure unimpaired productivity of the protected waters. This degree of protection is exceeded only by total exclusion of putrescible organic wastes and therefore no reduction of O_2 concentration below natural levels at any time. It requires, of course, either complete suspension of waste-producing operations or storage of all O_2-demanding wastes whenever the estimated natural seasonal minima occur naturally. Such periodic interruption of waste discharges is not often feasible, and for this reason we doubt that the level of protection represented by line A will be often chosen in preference to the maintenance of natural O_2 levels at all times, the highest possible level of protection.

The curves designated B and B_1 are appropriate, we suppose, to a high level of protection of fishery resources of such dominant importance that no uses of the water that are likely to cause considerable reduction of fish production can be approved. Some impairment of fish production doubtless is risked even when this high level of protection is provided, but the damage is not to be expected and can never be great, in our opinion. Curve B is intended for general application and curve B_1 for application to major spawning grounds of salmonid fishes during the months when embryos or larvae are in the gravel.

Curve C is supposed to be appropriate to moderate protection of fisheries that are highly valued but cannot be given more protection because they must coexist with major industries or a dense human population, or with both of these. With this level of protection, we would expect existing fisheries to persist and usually to suffer no serious impairment, but some reduction of fish production is likely to occur often, in our opinion.

Curve D is deemed appropriate to a low level of protection of fisheries that have some commercial or recreational value but are so unimportant, in comparison with other water uses, that their maintenance cannot be a major objective of pollution control. This level of protection is likely, we suppose, to permit the persistence of sizeable populations of some of the more tolerant species and successful passage of most migrants. However, we would expect much reduced production or even complete elimination of other, resident fishes, often the more desirable ones. Furthermore, use of this curve is not deemed appropriate when successful passage of the most sensitive migrants, such as the anadromous salmonids, must be ensured. Whenever unobstructed migration routes for such fishes are essential to the persistence of important fisheries, use of curve C or of an interpolated curve intermediate between curves C and D is recommended. In our opinion, interpolated values (acceptable O_2 concentration minima) about half-way between those obtained by using curves C and D will usually be adequate to ensure normal migration of salmonid fishes through lower reaches of most streams where the current velocity is moderate.

To apply the proposed criteria, it would be necessary, of course, to determine the natural, seasonal O_2 minimum from which the acceptable minimum is to be derived by reference to the appropriate curve in Figure 1. For waters that can be adequately studied before they are materially altered from their natural condition, the relations between season of the year, temperature, stream discharge volume, and O_2 concentration can be determined by observation. We suggest that, from these data, sufficiently reliable estimates probably can be derived of natural O_2 minima not only in these waters but also in other similar waters in the same geographical region when waste discharges render direct determination of natural O_2 levels impossible.

Unfortunately, in many densely populated regions, all or most of the larger streams and lakes have already been much altered from the natural condition by waste discharges and other human activities. If sufficient records of O_2 concentrations in such waters before these changes occurred are lacking, accurate determination of natural minima may be no longer possible. This will probably be the principle objection to the use of the proposed criteria as a basis for water quality standards. However, it is our view that errors in the choice of water quality standards that would result from incorrect estimation of natural conditions could not be as great as errors that are likely to result from total disregard of natural water quality differences. When the need for sound estimation of natural properties of waters receiving wastes if fully recognized, the necessary basic data and reliable methods doubtless will be developed. Some standardization of the methods may be feasible and desirable, but regulatory agencies will have to rely in large degree upon the judgment of groups (panels) of experts charged with the responsibility of determining the probable natural properties of particular waters. Members of these special panels should be unbiased so that their decisions would be acceptable to all interested parties.

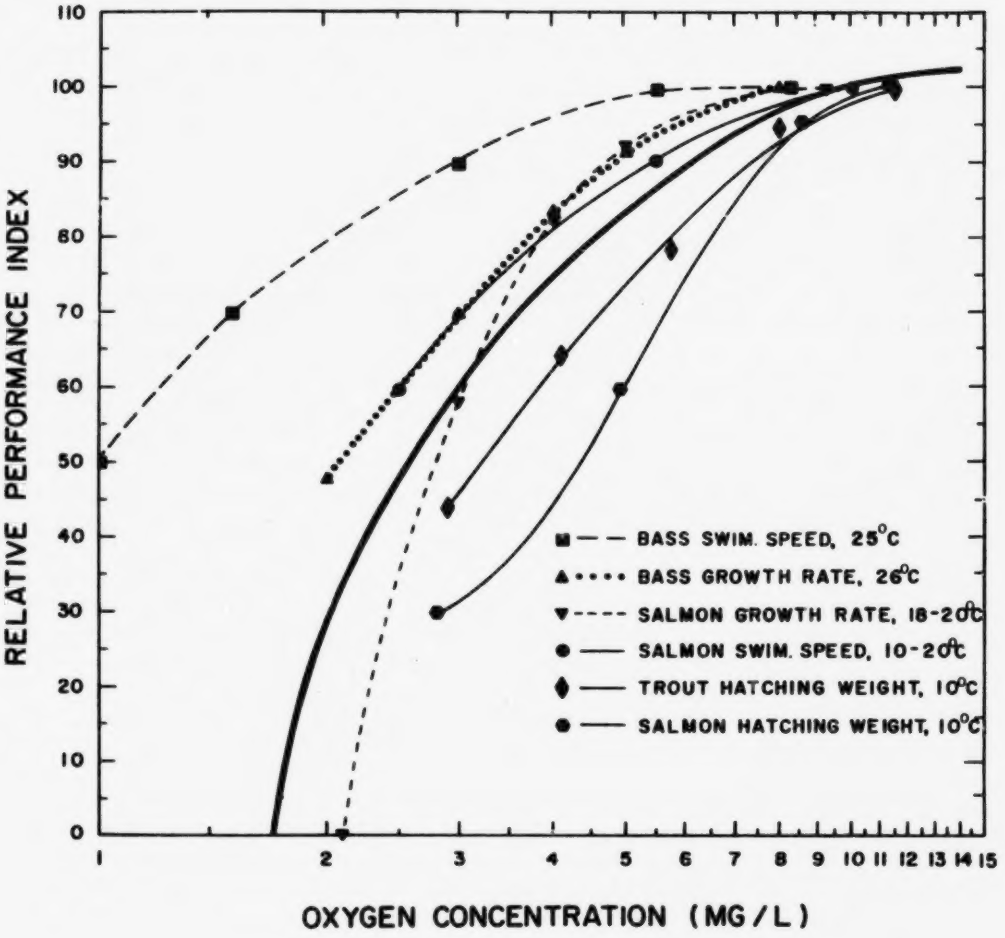
DERIVATION OF PROPOSED CRITERIA

The position of each of the several curves in Figure 1 has no demonstrable relation to any particular experimental results. It represents merely our best judgment broadly based on all of the pertinent information now available to us. Our curves are admittedly tentative, and substitution of similar curves lying somewhat above or below them could well be dictated by future experience in their application and by results of additional research.

The shaping of the curves in Figure 1, however, did have some connection with particular experimental data. Originally, these curves were drawn by us with a variety of general considerations in mind. But having drawn the original curves, we decided to test their general accordance with available data from laboratory experiments in which relative magnitudes of various readily quantifiable responses of fishes to different reductions of O_2 concentration had been reliably determined. Therefore, we plotted some curves by a different procedure which is indicated below, and we compared them with the original ones. It was interesting to find that curves arrived at in the two different ways very nearly coincided. We then decided to adopt the formal second procedure for derivation of the curves in Figure 1, except curve B_1. Explanation of the shaping of these curves thus was facilitated. We well realize, however, that the experimental data we have used have to do only with a few selected typical responses of individual organisms to reduction of O_2 concentration under controlled laboratory conditions. We do not wish to imply the assumption that quite different responses of fish populations under natural conditions will generally parallel these miscellaneous measured responses. We realize that natural production rates of fish populations, for example, cannot be reasonably assumed to vary with O_2 concentration in the same way as do growth rates of fish fed unrestricted rations in the laboratory. Still, we believe that our use of experimental data in deriving our own curves is not unreasonable in the absence of more relevant quantitative information.

In Figure 2, the experimental data that we decided to use, all obtained at moderately high temperatures, have been plotted together, and curves have been fitted by eye to the data. These curves show how the rates of growth on unrestricted rations and the sustained swimming speeds of coho salmon and largemouth bass, and also the weights of newly hatched coho salmon and steelhead trout alevins, were related to dissolved O_2 concentrations (or, strictly speaking, to their logarithms). The data used in plotting these curves are believed to be some of the best available data showing marked responses of experimental animals to moderate reductions of O_2 below air-saturation levels. They are all values (actual observations or values obtained by interpolation) reported in the text of this treatise. In graphing each set of data, the mean growth rate, swimming speed, or size at hatching at each

Figure 2. "Impairment-of-performance responses" of freshwater fishes to reductions of oxygen concentration: Hypothetical "average" concentration-response curve (heavy line) generally agreeing with some plotted, representative relations between oxygen concentration and indices of relative "performance" (growth rate, swimming speed, or weight at hatching) of largemouth bass, coho salmon, and steelhead trout. The plotted points are included mainly to facilitate identification of curves; they are all data reported somewhere in the text; some are actual observations, but most are estimates obtained by interpolation or by integration of experimental results. The significance of the ordinates ("relative performance indices") is explained in the text; they are percentages of values obtained at the air-saturation level of dissolved oxygen, except that in the case of the hypothetical concentration-response curve, the ordinates have no definite meaning. The indicated average oxygen concentration corresponding to no growth of coho salmon (zero ordinate) is a crude estimate.


RELATIVE PERFORMANCE INDEX
110
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
OXYGEN CONCENTRATION (MG/L)
■ — — BASS SWIM. SPEED, 25°C
▲ • • • • BASS GROWTH RATE, 26°C
▼ - - - - SALMON GROWTH RATE, 18-20°C
● —— SALMON SWIM. SPEED, 10-20°C
♦ —— TROUT HATCHING WEIGHT, 10°C
● —— SALMON HATCHING WEIGHT, 10°C

tested level of O_2 has been plotted as a percentage of the corresponding mean value for the air-saturation level. This percentage is designated the "relative performance index." The most prominent curve in Figure 2 (heavy line) is a curve that we have taken to be fairly representative of the entire group of response curves fitted to the plotted data. It is a generalized or "average" O_2 concentration-response curve representing no particular effect or response but agreeing in general with the various experimentally derived curves considered collectively. For this curve, the ordinates (relative performance indices) represent percentages of "performance" at the 9.5 mg/l level of O_2, a value near the average of the air-saturation levels of O_2 at the various experimental temperatures. The curve has been extended to the 14 mg/l levels of O_2, however, so that its highest ordinate is slightly greater than 100 (i.e., 102.5). We shall not attempt to explain here in detail the rather complex reasoning underlying the drawing of this curve; we hope that enough of it will be apparent to the reader after careful consideration of the matter. Admittedly, the depressing effects of O_2 reductions depicted by this curve probably are somewhat greater than most of the effects that have been observed at average temperatures of fresh waters of the Temperate Zone. As noted above, the data plotted in Figure 2 were obtained at moderately high temperatures. At low temperatures, some effects are evident only when reductions of O_2 concentration from saturation levels are relatively large. However, the bias resulting from the omission of low-temperature data is intentional, our purpose being to devise criteria appropriate to the protection of fish at the higher temperatures, and not only at average and lower temperatures.

Comparison of any one of the curves in Figure 1 except curve B_1 with the generalized response curve (heavy line) in Figure 2 will reveal a close relationship between them, a relationship not immediately apparent. Reductions of O_2 (from estimated natural seasonal minima) that are shown to be "acceptable" by curves A, B, C, and D in Figure 1 correspond to the following constant (along each curve) per cent reductions of ordinates in Figure 2: 0%, 3%, 9%, and 20%, respectively.

For example, let us consider curve C in Figure 1. It shows that a reduction of O_2 concentration from a natural seasonal minimum of 9.5 mg/l to the 6.3 mg/l level, or from a natural seasonal minimum of 6.1 mg/l to the 4.8 mg/l level is acceptable. Turning now to the curve in Figure 2, we find that a reduction of O_2 concentration (abscissa) from 9.5 mg/l to 6.3 mg/l corresponds to a reduction of the ordinate value from 100 to 91, or a 9% reduction. Likewise, a reduction of O_2 concentration (abscissa) from 6.1 mg/l to 4.8 mg/l corresponds to a reduction of the ordinate from 90 to 82, again about a 9% reduction (90 x .09 = 8). The same relationship will be found between curve B or curve D in Figure 1 and the generalized response curve in Figure 2, except that the percent reductions of Figure 2 ordinates will be 3% for curve A and 20% for curve D. For curve A, this reduction is, of course, nil. For the lower portion of the curve B_1 which was designed especially for application to very valuable salmonid spawning grounds when embryos or larvae are in the gravel, the reduction is about 1.5%. However, as noted earlier, this curve does not entirely conform to a formula like that used in plotting the other curves; its upper portion is less curved that it would have had to be to conform. Some special considerations led to our deviation from the regular procedure in shaping this curve.

In designing the proposed criteria, we have consciously disregarded in large degree the known variations with temperature of the O_2 requirements of fishes and of the solubility of O_2 in water. We realize that natural O_2 concentration minima are likely to be relatively high when the O_2 requirements of fishes are relatively low because of low water temperatures. We have made no provision, however, for adjustment of the acceptable O_2 minima for different seasons of the year according to temperature. Provision for such adjustment would have involved serious complication of the criteria, and after careful consideration we have decided that it is unnecessary.

The design of waste treatment and disposal facilities in accordance with our proposed criteria must be based usually on the assimilatory capacity of the receiving waters in summer, when the lowest O_2 concentrations are most likely to occur naturally. However, reduced O_2 concentrations that are acceptable in summer may be unsuitable for successful reproduction of some valuable fishes during another season of the year when temperatures are relatively low. That is, higher O_2 concentrations may be required during the cooler season to ensure successful spawning. Also most of the growth of fish, and the most rapid growth, may well occur when temperatures are not nearly maximal but natural foods and dissolved O_2 are abundant. These considerations are the main reasons for our recommendations that the acceptable O_2 minimum for a given water and season of the year be based on the estimated O_2 minimum for the season, rather than on the estimated annual minimum. They also had much to do with our decision to recommend no adjustments for water temperature.

In our Introduction, we have already indicated the reason why interactions between O_2 deficiency and toxicity of various pollutants that may be present in waters receiving putrescible organic wastes also have not been considered in formulating the recommended criteria. In our opinion, the disposal of toxic pollutants must be controlled so that their concentrations would not be unduly harmful at prescribed, acceptable levels of O_2, temperatures, and pH values. The acceptable O_2 levels, on the other hand, should be independent of existing or highest permitted concentrations of toxic wastes, no matter what may be the nature of interaction between these toxicants and O_2 deficiency.

Our decision to prescribe acceptable O_2 concentration minima, and not acceptable average concentrations, is based on various considerations. Among these are experimental data indicating that, when O_2 concentrations fluctuate widely about an apparently satisfactory mean level, adverse effects on the growth of fish, as well as on survival, can be pronounced. Another pertinent consideration is the difficulty of enforcement of water quality standards limiting average concentrations.

APPENDIX IV

TABLES FOR RESEARCH CONDUCTED FROM SEPTEMBER 1, 1968 THROUGH AUGUST 31, 1971

Table 1. Initial and final weights, growth and food consumption rates, and gross food conversion efficiencies of juvenile largemouth bass held in 12-gal bottles at different dissolved oxygen concentrations and temperatures. The bass were fed to repletion on small fish or tubificid worms.

Dissolved oxygen concentration (mg/liter)	Total wet weight (g)			Total dry weight (g)			Food consumption rate[1] (mg/g/day)	Mean growth rate[2] (mg/g/day)		Gross efficiency[3] (%)	Mean growth rate: Standard error		Mean growth rate: LSD .05[4]	
	Initial	Final	Difference	Initial	Final	Difference	Dry	Wet	Dry	Dry	Wet	Dry	Wet	Dry
Experiment 1, 10C, 6 fish, 30 days, April 10, 1969														
2.4	49.98	54.84	4.86	12.31	13.52	1.21	12.7	3.08	3.06	24.6	0.36	0.41		
3.7	48.96	56.28	7.32	12.05	13.85	1.80	15.6	4.71	4.64	29.9	0.53	0.44		
5.4	50.16	58.56	8.40	12.36	14.25	1.89	15.7	5.09	4.67	29.9	0.39	0.79		
9.0	51.24	57.84	6.60	12.61	14 40	1.79	14.1	4.03	4.50	31.3	0.49	0.55		
11.3	48.96	55.80	6.84	12.05	13.65	1.80	15.3	4.28	4.47	30.5	0.45	0.54	n.s.	n.s.
11.1[6]	49.50	57.54	8.04	12.19	14.58	2.39	22.7	5.01	5.94	26.2	0.49	0.63	-	-
Experiment 2, 15C, 6 fish, 25 days, April 23, 1969														
2.3	57.12	73.14	16.02	14.39	17.94	3.55	24.9	9.83	8.71	35.1	0.83	0.59	*	*
3.4	58.38	82.38	24.00	14.69	20.77	6.08	32.0	13.68	13.67	37.0	0.63	0.66		
4.8	53.46	82.68	23.22	14.98	20.48	5.50	32.2	13.08	12.50	38.9	0.91	0.93		
7.1	55.68	76.56	20.88	14.03	19.22	5.19	31.3	12.47	12.30	38.7	0.90	0.87		
10.0	58.50	82.44	23.94	14.73	20.45	5.72	32.2	13.57	12.97	40.4	1.09	1.20	2.58	2.57
9.9[6]	58.74	81.06	22.32	14.79	21.06	6.27	42.5	12.87	13.95	32.8	0.82	0 78	-	-
Experiment 3, 15C, 6 fish, 25 days, July 14, 1969														
2.5	81.60	99.72	18.12	20.82	26.04	5.22	20.0	7.89	8.83	44.6	0.95	0.81		
3.2	81.24	107.04	25.80	20.72	27.55	6.83	25.3	10.93	11.77	44.7	0.60	0.82		
4.6	80.82	109.26	28.44	20.60	28.35	7.74	29.6	11 92	12.54	42.7	1.02	1.27		
7.2	81.90	114.24	32.34	20.88	29.72	8.84	31.9	13.02	13.71	43.8	0.94	1.42		
10.3	82.92	108 0	25.58	21.14	28.28	7.14	26.8	10.50	10.96	43.1	2.19	2.05	n.s	n.s
10.1[6]	83.33	104.6[6]	21.33	21.24	27.32	6.08	42.2	9.00	10.36	23.7	0.74	0.99	-	-
Experiment 4, 20C, 6 fish, 20 days, July 14, 1969														
2.4	82.94	117.59	34.65	21.15	29.67	8.52	37.9	17.22	16.68	44.2	1.40	1.36	*	*
3.3	85.62	127.80	42.18	21.84	33.62	11.78	42.3	19.66	21.16	50.1	1.05	1.17	*	*
4.4	83.82	135.42	51.60	21.37	35.63	14.26	47.6	24.44	24.90	52.6	1.40	1.25	*	*
6.2	83.94	147.24	63.30	21.41	39.10	17.69	56.7	29.10	29.28	51.6	1.52	1.07		
9.0	84.84	152.16	67.32	21.64	41.19	19.55	58.8	28.21	30.98	52.9	1.05	0.99	3.75	3.39
9.4[6]	82.08	122.52	40.44	20.93	34.10	13.17	82.8	19.70	23.90	28.9	1.70	1.23	-	-
Experiment 5, 29.3C, 7 fish, 17 days, September 13, 1970[5]														
6.3	37.42	--	--	8.87	29.11	20.24	111.1	--	62.7	56.4				
5.3	34.87	--	--	8.26	25.40	17.14	112.1	--	59.9	53.4				
4.9	38.07	--	--	9.02	23.82	14.80	100.9	--	53.0	52.5				
4.0	39.88	--	--	9.45	14.41	4.96	83.6	--	24.5	29.3				
3.7	37.79	--	--	8.96	24.47	15.51	94.2	--	54.6	58.0				
2.8	37.57	--	--	8.90	19.87	10.97	96.4	--	44.8	46.5				
Experiment 6, 24.1C, 7 fish, 17 days, September 13, 1970[5]														
8.0	34.60	--	--	8.20	23.49	15.29	103.4	--	56.7	54.8				
6.0	39.78	--	--	9.43	27.68	18.25	101.1	--	57.8	57.2				
5.2	41.53	--	--	9.84	26.28	16.44	94.6	--	53.5	56.6				
4.6	38.16	--	--	9.04	22.57	13.53	95.6	--	50.3	52.6				
3.7	43.60	--	--	10.33	24.09	13.76	86.1	--	47.0	54.6				
2.8	40.71	--	--	9.65	21.55	11.90	86.3	--	44.9	52.0				

[1] Food consumption rates are expressed in milligrams per mean gram of tissue present ($\frac{\text{final weight plus initial weight}}{2}$) per day.

[2] Mean values are based on individual growth rates expressed as tissue elaborated in milligrams per mean gram of tissue ($\frac{\text{final weight plus initial weight}}{2}$) per day. In experiments 5 and 6, total weights of bass were used in determining mean growth rates.

[3] Gross food conversion efficiencies were determined using total weights of tissue elaborated and food consumed.

[4] Asterisk indicates growth rates that are significantly different from those of bass reared at near air-saturation and fed small fish.

[5] All fish died during the evening of the last test day; therefore, wet weights were not determined.

[6] Bass were fed live tubificid worms in this treatment, whereas those in other treatments were fed small fish.

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Table 2. Initial and final weights, weight gained, food consumption and growth rates, and gross food conversion efficiencies of juvenile largemouth bass held for 10 days at 20°C in 12-gal bottles. One, five, and ten fish were held in separate bottles and fed to repletion on small fish. All values are based on wet weights.

Number of bass per chamber	Total weight (g)			Food consumption rate[1/] (mg/$\bar{g}$/day)	Growth rate[1/] (mg/$\bar{g}$/day)	Gross efficiency (%)
	Initial	Final	Difference			
1	8.64	11.18	2.54	73.97	25.63	34.6
1	10.65	15.04	4.39	89.33	34.19	38.3
5	42.30	50.39	8.09	63.53	17.46	27.5
5	41.34	55.87	14.53	81.34	29.95	36.8
10	85.56	107.75	22.19	68.42	22.96	33.6
10	74.98	100.25	25.27	78.56	28.84	36.7

[1/] Growth and food consumption rates are expressed as tissue elaborated (or food consumed) in milligrams per mean gram of tissue present ($\frac{\text{final weight plus initial weight}}{2}$) per day.

Table 3. Initial and final weights, growth and food consumption rates and gross food conversion efficiencies of juvenile chinook salmon held in 12-gallon bottles at different temperatures and dissolved oxygen concentrations. The salmon received unrestricted rations of live tubificid worms.

Dissolved oxygen concentration (mg/liter)	Total wet weight (g)			Total dry weight (g)			Food consumption rate[1/] (mg/g/day)		Growth rate[1/] (mg/g/day)		Gross efficiency (%)	
	Initial	Final	Difference	Initial	Final	Difference	Wet	Dry	Wet	Dry	Wet	Dry
Experiment 1, 13.0C, 10 fish, 20 days, March 28, 1970												
10.7	21.0	52.0	31.0	4.2	11.7	7.4	157	117	43.0	46.6	27.3	39.8
8.3	21.4	51.5	30.1	4.3	11.6	7.3	155	115	41.3	45.8	26.7	39.9
6.4	21.0	50.3	29.3	4.2	11.3	7.0	155	116	41.1	45.3	26.5	39.2
4.9	20.6	49.5	28.9	4.2	11.1	6.9	151	113	41.2	45.4	27.3	40.2
3.9	20.5	47.0	26.5	4.1	10.4	6.3	142	106	39.3	43.2	27.7	42.6
3.1	21.3	43.3	22.0	4.3	9.7	5.3	121	90	34.1	38.3	28.2	42.4
Experiment 2, 8.4C, 10 fish, 20 days, March 28, 1970												
11.3	20.2	37.5	17.3	4.1	8.0	3.9	108	83	30.0	32.6	27.8	39.1
9.1	20.5	38.7	18.2	4.1	8.3	4.2	111	86	30.8	33.4	27.6	38.8
7.0	19.9	37.8	18.0	4.0	8.1	4.1	111	85	31.1	33.7	28.1	39.6
5.4	19.9	37.2	17.3	4.0	8.0	4.0	111	82	33.8	33.1	31.6	40.2
4.2	19.9	36.3	16.4	4.0	7.8	3.8	103	80	29.2	31.8	28.2	39.8
3.1	20.4	33.0	12.6	4.1	7.2	3.1	89	67	23.6	27.1	26.6	40.3
Experiment 3, 13.2C, 9 fish, 20 days, June 7, 1970												
10.8	7.2	18.6	11.4	1.3	4.0	2.7	183	177	44.2	50.9	24.1	28.8
8.4	7.4	19.7	12.4	1.3	4.3	3.0	171	165	45.6	52.3	26.7	31.7
6.4	7.2	17.7	10.5	1.3	3.7	2.4	162	161	41.9	47.8	25.9	29.6
5.2	7.4	16.9	9.5	1.4	3.5	2.2	160	161	39.1	44.5	24.4	27.7
3.9	7.3	14.9	7.6	1.3	3.1	1.8	136	138	34.1	39.8	25.0	28.9
3.3	7.2	13.9	6.7	1.3	2.8	1.5	124	126	31.5	36.5	25.5	29.0
Experiment 4, 17.8C, 9 fish, 20 days, June 7, 1970												
9.1	7.2	24.3	17.1	1.3	5.6	4.2	201	186	54.2	61.8	26.9	33.3
7.4	7.1	23.9	16.8	1.3	5.5	4.2	199	182	54.1	61.6	27.2	33.8
6.1	7.0	20.2	13.2	1.3	4.6	3.3	189	177	48.6	56.5	25.7	31.9
4.6	7.0	19.8	12.8	1.3	4.5	3.2	176	166	47.7	55.6	27.1	33.5
3.7	6.9	13.6	6.7	1.3	2.8	1.6	135	136	32.6	38.0	24.1	27.9
3.9	6.3	10.1	3.8	1.1	2.0	0.9	105	110	23.0	27.1	21.9	24.6
Experiment 5, 21.7C, 10 fish, 20 days, July 13, 1971												
7.3	14.5	27.9	13.3	2.7	6.0	3.3	183	147	29.0	36.7	15.8	25.0
6.7	14.7	30.4	15.8	2.7	6.6	3.9	191	151	33.3	40.3	17.4	26.6
5.4	15.8	25.6	9.9	2.9	5.4	2.6	147	119	22.7	29.4	15.5	24.7
3.8	15.3	18.8	3.5	2.8	3.8	1.0	121	102	9.9	14.5	8.2	14.2
3.3	80 percent mortality occurred during the test.											
Experiment 6, 18.6C, 10 fish, 20 days, July 13, 1971												
7.8	16.4	41.0	24.6	3.0	9.2	6.2	184	141	40.8	48.6	22.2	34.4
7.3	15.5	38.2	22.7	2.9	8.6	5.8	185	141	40.2	48.1	21.8	34.0
5.7	10.9	23.1	12.3	2.0	5.0	3.1	168	132	34.3	41.5	20.5	31.4
4.9	16.5	29.3	12.8	3.0	6.4	3.4	152	121	26.5	33.3	17.4	27.5
4.1	15.4	24.8	9.4	2.8	5.3	2.5	140	113	22.3	29.1	16.0	25.7
3.3	60 percent mortality occurred during the test.											

[1/] Growth and food consumption rates are expressed as tissue elaborated (or food consumed) in milligrams per mean gram of tissue present $\left(\frac{\text{final weight plus initial weight}}{2}\right)$ per day.

Table 4. Experimental conditions, weights, food consumption rates, growth rates, and gross food conversion efficiencies for juvenile chinook salmon during cyclic ration feeding studies. Ten fish were held in each test chamber.

Mean dissolved oxygen (mg/l)	Feeding level[1]	Total wet weight (g)			Total dry weight (g)			Food consumption rate (mg/$\bar{g}$/day)		Growth rate (mg/$\bar{g}$/day)		Gross efficiency %	
		Initial	Final	Diff.	Initial	Final	Diff.	Wet	Dry	Wet	Dry	Wet	Dry
Experiment 1, 12C, chinook salmon, 14 days, March 20, 1971													
10.4	L	18.65	21.22	2.57	3.51	3.95	0.44	57.2	52.1	9.2	8.4	16.1	16.1
5.1	L	18.87	21.06	2.19	3.55	3.97	0.42	51.8	52.8	7.8	8.0	15.1	15.2
3.1	L	18.33	20.06	1.73	3.45	3.85	0.41	44.8	49.9	6.4	7.8	14.3	15.6
10.3	H	19.65	27.43	5.03	3.69	4.90	1.21	74.5	70.1	16.3	20.1	21.9	28.7
5.0	H	19.02	24.37	5.35	3.58	4.88	1.30	76.1	71.0	17.3	22.0	23.2	30.9
2.9	H	18.89	22.06	3.17	3.55	4.35	0.80	55.8	54.3	11.1	14.5	19.9	26.7
Experiment 2, 17C, chinook salmon, 21 days, April 9, 1971													
9.1	L	20.17	24.90	4.73	3.87	4.59	0.72	83.3	75.8	9.9	8.1	12.0	10.7
4.9	L	20.62	25.96	5.34	3.96	4.91	0.95	78.8	72.1	10.9	10.2	13.8	14.1
3.3	L	19.68	24.58	4.90	3.78	4.68	0.91	73.9	65.1	10.5	10.2	14.7	15.7
9.0	H	19.72	29.02	9.30	3.78	5.73	1.95	105.9	98.4	18.2	19.5	17.1	19.8
4.5	H	20.44	30.69	10.25	3.92	6.16	2.24	98.9	87.3	19.1	21.1	19.3	24.7
3.2	H	20.87	30.57	9.70	4.00	6.18	2.18	91.9	80.8	18.0	20.4	19.5	25.2

Table 4. Continued

Mean dissolved oxygen (mg/l)	Feeding level[1/]	Total wet weight (g)			Total dry weight (g)			Food consumption rate (mg/g/day)		Growth rate (mg/g/day)		Gross efficiency %	
		Initial	Final	Diff.	Initial	Final	Diff.	Wet	Dry	Wet	Dry	Wet	Dry
Experiment 2, 12 C, chinook salmon, 21 days, April 9, 1971													
10.7	L	19.62	25.21	5.59	3.76	4.75	0.99	71.5	65.6	11.9	11.0	16.6	16.8
5.0	L	21.00	27.64	6.64	4.03	5.32	1.29	65.6	59.4	13.0	13.1	19.8	22.1
3.3	L	20.20	26.32	6.12	3.87	5.15	1.27	63.0	56.6	12.6	13.4	19.9	23.7
10.6	H	18.32[2/]	28.87	10.55	3.63	5.79	2.16	91.5	83.3	21.3	23.0	23.3	27.6
5.0	H	22.33[2/]	34.20	11.87	4.42	6.78	2.36	79.4	73.3	20.0	21.0	25.2	28.6
3.0	H	20.94	31.77	10.83	4.02	6.31	4.44	81.0	70.0	19.6	21.1	24.8	30.1

[1/] Daily ration fed each week: L= 0, 1, 3, R, R, 3, and 1%
H= 3, 4, 6, R, R, 6, and 4% of initial wet weight of salmon (R= repletion)

[2/] Nine fish were placed in the bottle at the oxygen concentration of 10.6 mg/l; eleven fish were placed in the bottle held at 5.0 mg/l of oxygen. The error was not discovered until the termination of the experiment.

Table 5. Initial and final weights, food consumption and growth rates, and food conversion efficiencies of juvenile coho salmon held in 12-gal bottles at various dissolved oxygen concentrations and temperatures. The salmon received an unrestricted supply of live tubificid worms.

Dissolved oxygen concentration (mg/liter)	Total wet weight (g)			Total dry weight (g)			Food consumption rate[1] (mg/ḡ/day)		Growth rate[1] (mg/ḡ/day)		Gross efficiency (%)	
	Initial	Final	Difference	Initial	Final	Difference	Wet	Dry	Wet	Dry	Wet	Dry
Experiment 1, 13.0C, 6 fish, 18 days, October 1, 1969												
3.0	34.40	44.40	10.00	7.62	10.69	3.07	-	71.3	14.10	18.63	-	26.1
3.7	33.20	45.80	12.60	7.34	11.27	3.93	-	78.7	17.72	23.46	-	29.8
5.4	34.60	53.40	18.80	7.67	13.22	5.55	-	97.2	23.74	29.52	-	30.5
8.3	34.10	57.50	23.40	7.56	14.47	6.91	-	109.8	28.38	34.85	-	31.7
10.9	33.70	57.40	23.70	7.46	14.58	7.12	-	116.5	28.91	35.89	-	30.8
21.5	33.00	56.50	23.50	7.30	14.30	7.00	-	119.9	29.17	36.01	-	30.0
Experiment 2, 18.0C, 6 fish, 13 days, October 1, 1969												
3.0	40.00	44.90	4.90	8.90	10.20	1.30	-	93.4	8.88	10.47	-	11.4
3.8	39.50	48.80	9.30	8.80	11.50	2.70	-	93.5	16.20	20.46	-	22.6
5.2	40.40	51.60	11.20	8.90	12.80	3.90	-	125.3	18.72	27.65	-	26.3
6.9	39.40	54.30	14.90	8.70	13.40	4.70	-	125.6	24.46	32.72	-	25.6
9.6	40.70	60.00	19.30	9.00	14.70	5.70	-	140.6	29.48	37.00	-	26.4
20.8	40.50	58.50	18.00	9.00	14.60	5.60	-	137.8	27.97	36.50	-	26.6
Experiment 3, 12.9C, 10 fish, 20 days, May 9, 1970												
10.8	10.23	26.50	16.27	1.85	6.04	4.19	179.7	159.6	44.3	53.0	24.6	33.2
8.3	9.71	27.16	17.45	1.76	6.12	4.36	175.3	156.7	47.3	55.3	27.0	35.3
6.6	9.76	23.49	13.73	1.77	5.37	3.60	166.8	148.4	41.3	50.4	24.7	34.0
5.1	9.88	24.16	14.28	1.79	5.44	3.65	160.1	143.8	42.0	50.4	26.2	35.1
3.9	10.15	20.91	10.76	1.84	4.68	2.84	141.6	128.8	34.6	43.5	24.5	33.8
3.1	10.05	17.85	7.80	1.82	3.95	2.13	124.0	114.3	28.0	36.8	22.5	32.2
Experiment 4, 8.6C, 10 fish, 20 days, May 1, 1970												
11.8	12.0	23.1	11.1	2.3	4.9	2.6	130.0	119.9	31.5	36.5	24.2	30.4
9.4	12.7	25.0	12.3	2.4	5.3	2.9	112.8	108.5	32.7	37.5	27.8	34.6
7.1	12.4	23.5	11.1	2.4	5.0	2.6	113.0	104.5	30.7	35.4	27.2	33.9
5.5	12.3	22.9	10.6	2.3	4.9	2.6	112.6	103.7	30.3	35.5	26.9	34.3
4.1	12.5	21.8	9.3	2.4	4.6	2.2	105.0	98.3	27.2	31.6	25.9	32.2
3.1	12.4	20.0	7.6	2.4	4.2	1.8	96.8	91.0	23.5	27.7	24.3	30.4
Experiment 5, 21.6C, 7 to 9 fish, 20 days, July 22, 1970[1]												
9.2	2.53	3.91	1.38	0.52	0.97	0.45	149.7	107.6	21.4	30.2	14.3	28.1
7.0	2.28	3.34	1.06	0.47	0.77	0.30	149.8	114.1	18.9	23.2	12.6	20.3
5.5	1.79	3.07	1.28	0.37	0.71	0.34	161.5	122.1	26.3	31.5	16.3	25.8
4.9	2.20	3.48	1.28	0.45	0.84	0.39	137.2	101.4	22.5	30.2	16.4	29.8
3.6	2.53	2.09	-0.44	0.52	0.46	-0.06	-	-	- 9.5	- 6.1	-	-
3.1	all died within the first ten days of the test											
Experiment 6, 18.0C, 7 to 9 fish, 20 days, July 22, 1970[1]												
7.2	2.32	3.74	1.42	0.47	0.90	0.43	128.6	95.5	23.4	31.4	18.2	32.9
5.8	2.19	3.78	1.59	0.45	0.91	0.46	136.4	100.7	26.6	33.8	19.5	33.6
5.1	2.47	4.23	1.76	0.50	1.03	0.53	134.0	98.5	26.3	34.6	19.6	35.1
4.0	2.14	3.56	1.42	0.44	0.85	0.41	120.9	89.7	24.9	31.8	20.6	35.5
3.1	2.18	3.00	0.82	0.44	0.71	0.27	115.7	61.3	15.8	[illegible]	13.7	38.3
9.7	2.06	3.60	1.54	0.42	0.85	0.42	150.7	113.5	27.2	33.3	18.0	29.3
Experiment 7, 21.8C, 9 fish, 20 days, June 15, 1971												
8.9	5.27	17.79	12.52	0.92	3.88	2.96	243.1	161.1	51.7	58.7	21.3	36.4
7.9	5.10	15.75	10.65	0.88	3.32	2.44	239.7	164.4	48.6	55.3	20.3	33.6
5.9	5.10	17.97	12.87	0.88	3.88	3.00	230.9	154.5	53.1	60.0	23.0	38.8
4.8	4.05	10.95	6.90	0.70	2.21	1.51	236.8	168.0	43.8	49.2	18.5	29.3
3.8	5.60	15.51	9.91	0.97	3.02	2.05	200.9	146.4	44.7	48.8	22.2	33.3
3.4	5.00	11.14	6.14	0.87	2.27	1.40	190.2	135.0	36.2	42.5	19.0	31.5
Experiment 8, 18.3C, 10 fish, 20 days, June 15, 1971												
9.3	5.42	22.56	17.14	0.94	5.02	4.08	246.6	159.8	58.3	65.2	23.6	40.8
7.5	5.89	19.68	13.79	1.02	4.37	3.35	231.0	151.0	51.3	59.1	22.2	39.1
6.1	5.82	16.15	10.33	1.01	3.49	2.48	219.9	148.1	44.8	52.5	20.4	35.4
5.0	5.94	22.13	16.19	1.03	4.94	3.91	225.0	145.9	54.9	62.3	24.4	42.7
3.9	5.72	20.24	14.52	0.99	4.40	3.41	223.9	148.5	53.3	60.7	23.8	40.5
3.6	5.80	6.31	0.51	1.00	1.26	0.26	-- [3]	--	0.4	11.0	--	--

[1] Growth and food consumption rates are expressed as tissue elaborated (or food consumed) in milligrams per mean gram of tissue present $\left(\frac{\text{final weight plus initial weight}}{2}\right)$ per day.

[2] The weights shown are mean weights. Mortality during acclimation reduced the initial number of fish per bottle to seven or nine.

[3] Four fish died during the experiment and therefore consumption rates were not determined.

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Table 6. Food consumption, growth rates, and food conversion efficiencies for juvenile coho salmon held individually in 1.5 liter plexiglas containers and fed various rations (percent of the wet body weight of the individual fish) of housefly larvae for 14 days. During the three seasons of the study, the temperature was maintained at 15C and the dissolved oxygen concentration was kept at 3, 5 or 8 mg/liter (see footnote).

Dissolved oxygen concentration (mg/liter)	Daily food ration1/ (%)	Wet weight (g)			Dry weight (g)			Food consumption rate2/ (mg/g/day)		Growth rate2/ (mg/g/day)		Gross efficiency (%)	
		Initial	Final	Difference	Initial	Final	Difference	Wet	Dry	Wet	Dry	Wet	Dry
	Summer 1968												
8.0	0	1.10	0.95	-0.15	0.24	0.16	-0.08	0	0	- 9.9	-27.1	-	-
	0	1.08	0.97	-0.10	0.23	0.18	-0.06	0	0	- 7.1	-19.6	-	-
	1	1.15	1.13	-0.03	0.25	0.24	-0.01	11.0	11.1	- 1.8	- 2.3	-	-
	1	0.91	0.86	-0.05	0.20	0.16	-0.03	10.5	12.2	- 3.9	-13.0	-	-
	2	1.38	1.46	0.08	0.30	0.30	0.01	19.8	20.7	4.2	1.2	21.0	5.4
	2	0.84	0.87	0.02	0.18	0.18	0.00	20.2	22.0	2.0	- 0.4	10.0	-
	3	1.05	1.11	0.05	0.23	0.23	0.01	31.2	31.8	3.5	1.6	11.3	4.5
	3	0.91	0.97	0.06	0.20	0.20	0.01	28.9	31.8	4.6	2.5	16.1	7.9
	4	1.17	1.36	0.19	0.25	0.29	0.03	37.3	37.7	10.7	9.0	28.6	22.1
	4	1.19	1.34	0.15	0.26	0.29	0.03	37.5	40.6	8.5	7.9	22.7	19.5
	5	1.29	1.53	0.24	0.28	0.32	0.04	45.9	46.9	12.2	9.4	26.5	18.5
	5	1.08	1.27	0.18	0.23	0.28	0.05	46.6	49.3	11.0	13.0	23.6	26.4
	R	1.40	2.09	0.70	0.30	0.47	0.17	97.2	93.4	28.5	31.3	29.3	31.2
	R	1.31	1.69	0.37	0.29	0.41	0.12	75.8	74.1	17.8	25.3	23.4	34.2
	R	1.09	1.40	0.31	0.24	0.31	0.08	65.7	62.6	17.5	20.0	26.6	29.3
	R	0.82	1.12	0.31	0.18	0.24	0.06	79.3	84.6	22.5	21.1	28.4	24.9
5.0	0	1.39	1.29	-0.10	0.28	0.23	-0.05	0	0	- 5.5	-14.4	-	-
	0	1.62	1.46	-0.16	0.33	0.29	-0.04	0	0	- 7.2	- 9.2	-	-
	1	1.19	1.15	-0.04	0.24	0.23	-0.01	10.9	12.6	- 2.3	- 2.6	-	-
	1	1.04	1.00	-0.04	0.21	0.19	-0.02	10.1	11.9	- 3.0	- 7.0	-	-
	2	0.86	0.86	0.01	0.18	0.17	-0.01	19.9	23.3	0.4	- 3.7	2.1	-
	2	1.27	1.31	0.04	0.26	0.28	0.02	19.6	21.8	2.4	4.2	11.3	19.5
	3	1.46	1.60	0.14	0.30	0.34	0.04	29.3	32.8	6.6	8.5	22.6	26.0
	3	1.31	1.41	0.10	0.27	0.30	0.04	28.9	32.0	5.3	9.0	18.2	28.1
	4	1.04	1.22	0.18	0.21	0.27	0.05	37.7	41.4	11.2	15.2	29.6	36.7
	4	1.04	1.15	0.11	0.21	0.26	0.04	38.8	42.1	7.0	13.3	18.2	31.7
	5	1.16	1.40	0.24	0.24	0.31	0.07	45.4	49.3	13.2	18.8	29.0	38.1
	5	1.18	1.44	0.26	0.24	0.32	0.07	45.5	49.9	13.9	18.9	30.5	37.9
	R	1.65	2.27	0.62	0.34	0.52	0.18	78.8	81.9	22.7	30.6	28.8	37.3
	R	1.12	1.45	0.32	0.23	0.33	0.10	71.8	75.2	17.9	26.4	24.9	35.0
	R	1.05	1.49	0.44	0.21	0.33	0.11	78.3	81.7	24.8	29.8	31.6	36.5
	R	1.01	1.32	0.31	0.21	0.33	0.12	80.0	80.0	19.1	32.4	23.8	40.5
3.0	0	1.01	0.94	-0.07	0.22	0.18	-0.04	0	0	- 5.2	-13.6	-	-
	0	0.87	0.80	-0.07	0.19	0.16	-0.03	0	0	- 6.0	-11.5	-	-
	1	1.43	1.43	0.00	0.31	0.28	-0.03	10.0	11.3	- 0.2	- 7.0	-	-
	1	1.08	1.05	-0.03	0.23	0.21	-0.02	10.6	11.9	- 0.2	- 7.7	-	-
	2	1.12	1.16	0.04	0.24	0.24	0.00	19.9	21.8	2.4	0.0	11.9	-
	2	0.96	0.98	0.02	0.21	0.19	-0.01	19.9	22.4	1.2	- 5.0	5.9	-
	3	1.33	1.38	0.05	0.29	0.29	0.00	29.8	32.5	2.4	- 0.5	8.2	-
	3	0.88	0.95	0.07	0.19	0.20	0.01	29.1	31.7	5.6	3.3	19.3	10.3
	4	1.02	1.16	0.14	0.22	0.26	0.04	37.0	39.0	8.9	10.4	23.9	26.7
	4	0.72	0.83	0.11	0.16	0.16	0.00	35.0	39.8	10.3	1.8	29.6	4.5
	5	1.01	1.18	0.17	0.22	0.25	0.03	42.2	46.3	11.1	8.6	26.4	18.5
	5	1.11	1.27	0.15	0.24	0.28	0.03	47.8	51.0	9.1	9.4	19.1	18.4
	R	1.33	1.66	0.33	0.29	0.36	0.07	56.1	59.1	15.8	15.6	28.2	26.5
	R	1.12	1.28	0.17	0.24	0.27	0.03	41.4	44.8	10.1	7.3	24.3	16.3
	R	1.31	1.63	0.32	0.28	0.37	0.08	58.4	62.6	15.6	18.2	26.7	29.0
	R	1.35	1.60	0.24	0.29	0.36	0.07	44.9	45.9	11.8	15.0	26.4	32.7
	Fall 1968												
8.0	0	1.91	1.63	-0.28	0.40	0.31	-0.09	0	0	-11.3	-17.2	-	-
	0	1.83	1.56	-0.27	0.38	0.25	-0.13	0	0	-11.4	-29.0	-	-
	1	3.03	2.93	-0.10	0.63	0.56	-0.08	10.2	15.9	- 2.5	- 9.3	-	-
	1	2.10	2.01	-0.09	0.44	0.43	-0.01	10.3	15.6	- 3.2	- 1.5	-	-
	2	3.00	3.00	0.00	0.62	0.61	-0.01	20.3	30.7	0.0	- 1.1	-	-
	2	2.59	2.60	0.02	0.54	0.52	-0.02	20.8	31.9	10.4	- 2.6	2.0	-
	3	2.44	2.71	0.27	0.51	0.57	0.06	28.3	42.5	7.6	8.3	26.7	19.4
	3	2.27	2.45	0.18	0.47	0.49	0.02	29.0	57.4	5.4	3.1	18.7	5.4
	4	2.96	3.52	0.56	0.61	0.74	0.13	36.6	54.1	12.3	13.6	33.6	25.1
	4	3.63	4.07	0.44	0.75	0.91	0.16	37.8	54.6	8.1	13.6	21.5	24.9
	5	2.53	3.11	0.59	0.52	0.68	0.14	45.7	67.4	14.8	17.1	32.5	25.4
	5	1.66	1.97	0.31	0.34	0.41	0.07	45.7	68.4	12.2	14.1	26.7	19.6
	R	2.89	4.07	1.19	0.60	0.91	0.31	65.0	92.5	24.4	29.5	37.5	31.9
	R	2.34	3.26	0.92	0.48	0.72	0.23	67.3	95.4	23.5	27.6	35.0	29.0
	R	2.44	3.37	0.94	0.50	0.80	0.30	64.0	87.5	23.0	32.6	35.9	37.3
	R	2.10	2.90	0.81	0.43	0.70	0.26	65.1	90.6	23.1	33.3	35.5	36.8
5.0	0	2.94	2.60	-0.34	0.61	0.53	-0.08	0	0	- 8.7	- 9.4	-	-
	0	1.85	1.60	-0.25	0.38	0.29	-0.0	0	0	-10.5	-18.8	-	-
	1	2.66	2.56	-0.10	0.55	0.46	-0 09	10.6	17.1	- 2.8	-13.2	-	-
	1	2.45	2.37	-0.07	0.51	0.53	0.03	10.3	14.7	- 2.2	3.6	-	24.3
	2	2.54	2.65	0.11	0.53	0.53	0.01	19.9	30.4	3.1	1.2	15.8	4.0
	2	2.30	2.30	-0.01	0.48	0.46	-0.12	20.8	32.1	- 0.2	- 2.8	-	-
	3	3.18	3.45	0.26	0.66	0.73	0.07	29.2	43.1	5.6	7.6	19.3	17.6
	3	3.14	3.48	0.34	0.65	0.78	0.13	29.0	41.2	7.3	12.7	25.8	30.8
	4	2.53	2.94	0.42	0.52	0.63	0.11	37.2	54.6	10.9	13.7	29.4	25.1
	4	3.56	4.18	0.62	0.74	0.88	0.14	37.8	55.1	11.4	12.9	30.9	23.1
	5	3.01	3.80	0.79	0.62	0.87	0.24	44.5	63.4	16.6	23.3	37.2	36.8
	5	2.65	3.27	0.62	0.55	0.71	0.16	45.7	65.9	15.0	18.1	33.5	27.5
	R	2.11	2.68	0.58	0.44	0.63	0.20	56.3	76.5	17.2	26.4	30.6	34.6
	R	2.28	3.09	0.81	0.47	0.71	0.24	61.5	86.1	21.5	28.4	34.9	33.1
	R	1.91	2.72	0.81	0.40	0.58	0.19	59.6	88.1	24.9	27.4	41.7	31.1
	R	1.94	2.96	1.02	0.40	0.68	0.28	77.8	107.6	29.7	35.8	38.2	33.8
3.0	0	2.54	2.22	-0.32	0.53	0.39	-0.14	0	0	- 9.6	-22.1	-	-
	0	2.95	2.65	-0.30	0.61	0.54	-0.07	0	0	- 7.8	- 8.4	-	-
	1	2.15	2.07	-0.08	0.45	0.41	-0.03	10.8	16.5	- 2.7	- 5.5	-	-
	1	3.22	2.94	-0.28	0.67	0.54	-0.13	10.5	16.9	- 6.5	-15.4	-	-
	2	3.13	3.22	0.09	0.65	0.67	0.03	29.9	30.0	2.1	2.4	10.3	9.0
	2	1.84	1.88	0.04	0.38	0.39	0.00	20.2	30.6	1.6	0.7	7.8	2.4
	3	1.99	2.18	0.18	0.41	0.47	0.06	29.2	43.0	6.3	8.9	21.5	20.8
	3	2.50	2.79	0.30	0.52	0.60	0.08	28.7	42.3	8.0	10.0	27.8	23.7

Table 6. Continued

Dissolved oxygen concentration (mg/liter)	Daily food ration[1/] (%)	Wet weight (g)			Dry weight (g)			Food consumption rate[2/] (mg/g/day)		Growth rate[2/] (mg/g/day)		Gross efficiency (%)	
		Initial	Final	Difference	Initial	Final	Difference	Wet	Dry	Wet	Dry	Wet	Dry
	Fall 1968												
3.0	4	4.10	4.61	0.52	0.85	1.06	0.22	37.7	53.4	8.5	16.1	22.5	30.1
	4	3.25	3.64	0.30	0.67	0.80	0.13	38.0	55.0	8.0	12.6	21.1	22.8
	5	3.20	3.74	0.54	0.66	0.84	0.18	43.9	62.6	11.1	16.6	25.3	26.6
	5	2.66	3.14	0.48	0.55	0.71	0.16	43.3	60.9	11.8	18.4	27.4	30.2
	R	1.94	2.47	0.53	0.40	0.58	0.17	67.4	93.4	17.1	25.4	25.4	27.2
	R	1.95	2.33	0.38	0.41	0.50	0.09	54.2	79.0	12.6	14.7	23.2	18.6
	R	2.69	3.53	0.84	0.56	0.77	0.22	57.1	82.4	19.3	23.3	33.9	28.3
	R	3.31	4.06	0.75	0.69	0.90	0.22	46.8	66.2	14.6	19.6	31.2	29.6
	Spring 1969												
8.0	0	5.52	4.93	-0.59	1.10	0.87	-0.23	0	0	- 7.0	-16.8	-	-
	0	4.68	3.82	-0.86	0.94	0.63	-0.31	0.4	0.6	-14.5	-28.4	-	-
	1	4.74	4.52	-0.22	0.95	0.94	-0.01	10.3	14.5	- 3.4	- 0.8	-	-
	1	4.93	4.69	-0.24	0.99	0.90	-0.09	10.4	15.4	- 3.6	- 6.8	-	-
	2	4.91	5.00	0.09	0.98	1.04	0.06	20.2	28.4	1.3	4.2	6.4	14.9
	2	5.30	5.34	0.04	1.06	1.15	0.09	20.3	28.1	0.5	5.8	2.7	20.8
	3	5.90	6.38	0.48	1.18	1.39	0.21	29.0	39.9	5.6	11.7	19.3	22.4
	3	6.15	6.53	0.38	1.23	1.31	0.08	29.2	41.8	4.3	4.5	14.7	10.8
	4	4.63	5.26	0.63	0.93	1.11	0.18	37.9	52.7	9.1	12.6	24.0	24.0
	4	4.04	4.64	0.60	0.81	1.03	0.22	37.7	51.0	9.9	17.1	26.2	33.5
	5	6.08	7.16	1.08	1.22	1.70	0.48	46.6	60.6	11.7	23.5	25.0	38.8
	5	6.73	8.14	1.41	1.35	2.08	0.73	45.7	57.0	13.6	30.5	29.6	53.5
	R	4.49	5.86	1.37	0.90	1.37	0.47	72.0	94.5	18.9	29.7	26.3	31.4
	R	4.67	6.32	1.65	0.93	1.58	0.65	70.1	88.4	21.5	37.1	30.6	42.0
	R	7.42	9.39	1.97	1.48	2.18	0.70	63.5	83.6	16.8	27.3	26.4	32.7
	R	6.72	10.35	3.63	1.34	2.57	1.23	82.1	103.1	30.4	45.0	37.0	43.7
5.0	0	4.03	3.36	-0.67	0.81	0.66	-0.15	0	0	-13.0	-14.8	0	0
	0	4.44	3.97	-0.47	0.89	0.76	-0.13	0.3	0.4	- 8.0	-11.3	-	-
	1	4.64	4.37	-0.27	0.93	0.89	-0.04	10.4	14.7	- 4.3	- 3.1	-	-
	1	4.95	4.70	-0.25	0.99	0.96	-0.03	10.5	14.9	- 3.7	- 2.2	-	-
	2	4.58	4.74	0.16	0.92	0.97	0.05	20.1	28.6	2.5	3.8	12.2	13.3
	2	5.73	5.80	0.07	1.15	1.29	0.14	20.4	27.6	0.9	8.2	4.3	29.7
	3	5.44	5.84	0.40	1.09	1.28	0.19	29.4	40.4	5.1	11.5	17.2	28.4
	3	5.32	5.72	0.40	1.06	1.28	0.22	29.4	39.7	5.2	13.4	17.6	33.8
	4	4.83	5.51	0.68	0.97	1.26	0.29	37.7	50.5	9.4	18.7	24.9	37.0
	4	3.65	4.14	0.49	0.73	0.90	0.17	38.0	52.4	9.0	15.0	23.7	28.6
	5	4.87	5.86	0.99	0.97	1.39	0.42	46.0	59.9	13.2	25.4	28.7	42.4
	5	4.39	5.09	0.70	0.88	1.12	0.24	46.5	63.3	10.6	17.1	22.7	27.1
	R	4.89	7.30	2.41	0.98	1.76	0.78	80.0	102.0	28.3	40.7	35.4	39.9
	R	4.77	6.94	2.17	0.95	1.71	0.76	76.4	96.4	26.5	40.8	34.7	42.3
	R	6.70	8.85	2.15	1.34	2.09	0.75	65.3	85.0	19.8	31.3	30.3	36.8
	R	6.20	8.90	2.70	1.24	2.28	1.04	74.4	91.6	25.5	42.2	34.3	46.1
3.0	0	4.90	4.29	-0.61	0.98	0.81	-0.17	0	0	- 9.5	-13.6	-	-
	0	4.72	Dead										
	1	4.88	4.51	-0.37	0.98	1.00	0.02	10.7	14.6	- 5.6	1.4	-	9.9
	1	4.81	4.61	-0.20	0.96	0.91	-0.05	10.4	15.1	- 3.0	- 3.8	-	-
	2	4.31	4.34	0.03	0.86	0.93	0.07	20.3	28.3	0.5	5.6	2.4	19.8
	2	4.98	5.03	0.05	1.00	1.08	0.08	20.7	28.6	0.7	5.5	3.5	19.2
	3	4.74	5.12	0.38	0.95	1.08	0.13	29.1	40.8	5.5	9.2	18.9	22.5
	3	5.07	5.38	0.31	1.01	1.22	0.21	29.5	39.8	4.2	13.5	14.4	33.9
	4	3.90	4.40	0.50	0.78	1.00	0.22	37.9	50.7	8.6	17.7	22.7	34.8
	4	5.56	6.29	0.73	1.11	1.48	0.37	37.7	49.7	8.8	20.5	23.3	41.2
	5	5.97	6.82	0.85	1.19	1.45	0.26	47.1	65.5	9.5	14.1	20.2	21.5
	5	5.70	6.25	0.55	1.14	1.35	0.21	44.9	61.7	6.6	12.1	14.7	19.6
	R	3.60	4.80	1.20	0.72	1.09	0.37	61.3	82.1	20.4	29.4	33.3	35.8
	R	4.11	4.95	0.84	0.82	1.13	0.31	51.5	69.1	13.2	22.8	25.7	33.0
	R	7.73	11.01	3.28	1.55	2.59	1.04	63.8	82.9	25.0	35.9	39.2	43.3
	R	7.02	8.05	1.03	1.40	1.93	0.53	44.0	57.3	9.8	22.8	22.2	39.8

[1/] "R" means repletion. These fish were allowed to consume as much food as they would at each daily feeding.

[2/] Growth and food consumption rates are expressed as tissue elaborated (or food consumed) in milligrams per mean gram of tissue present ($\frac{\text{final weight plus initial weight}}{2}$) per day.

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Table 7 Mean and range of temperature and dissolved oxygen concentration, prey density, and lengths, weights and growth rates of largemouth bass for the pond experiments.

Experiment number and date	Mean temperature and range (°C)	Mean dissolved oxygen and range (mg/l)	Initial prey density (g/pond)	Total length (cm)		Wet weight (g)			Growth rate mg/g/day
				Initial	Final	Initial	Final	Difference	
1 10/13/70	13.3 (11.5-14.7)	4.2 (3.7- 5.4)	170	11.9	12.4	20.7	24.0	3.3	10.5
				11.9	12.4	20.0	22.7	2.7	8.6
				11.7	12.3	19.7	23.9	4.2	13.9
				11.6	12.2	19.6	23.3	3.7	12.3
	13.3 (11.6-15.6)	10.4 (10.2-10.9)	170	11.7	12.1	19.7	23.6	3.9	12.8
				11.8	12.2	19.9	24.2	4.3	13.9
				11.7	12.1	19.4	22.0	2.6	8.5
				11.6	12.2	19.2	22.1	2.9	9.9
2 11/18/70	13.3 (11.7-15.5)	4.2 (3.8- 5.7)	170	11.8	12.2	20.3	23.6	3.3	10.7
				11.6	11.9	19.6	23.4	3.8	12.7
				11.6	12.1	19.2	22.4	3.2	11.1
				11.7	12.5	19.8	22.8	3.0	10.0
	13.9 (12.8-16.1)	10.3 (10.1-10.8)	170	11.5	11.8	18.4	20.8	2.4	8.9
				12.0	12.1	19.9	24.0	4.1	13.4
				11.8	12.3	20.7	24.2	3.5	11.1
				11.7	11.9	20.3	24.7	4.4	13.9
3 9/25/70	16.0 (13.8-17.2)	4.7 (3.7- 5.6)	170	11.8	12.6	20.3	25.1	5.0	15.6
				11.6	12.4	19.1	24.1	5.0	16.4
				11.4	12.6	17.4	21.9	4.5	16.3
				11.6	12.5	20.3	24.7	4.3	13.7
	16.6 (13.2-19.6)	9.6 (9.4-10.4)	170	11.8	12.5	18.2	24.7	6.4	21.4
				11.7	12.7	19.4	25.6	6.3	19.9
				11.5	12.2	18.9	24.5	5.6	18.5
				11.7	12.8	20.4	26.2	5.8	17.7
4 4/12/71	16.6 (15.2-19.1)	6.0 (5.2- 7.1)	170	11.5	12.1	18.3	22.6	4.3	15.2
				11.5	12.3	18.2	23.3	5.1	17.4
				11.6	12.2	18.6	23.8	5.2	17.5
				11.6	12.3	18.1	23.0	5.0	17.2
	16.8 (14.3-20.7)	9.6 (9.3-10.2)	170	11.6	12.6	18.9	24.7	5.7	19.2
				11.5	12.2	18.4	23.5	5.1	17.4
				11.7	12.4	18.8	25.6	6.8	21.8
				11.7	12.5	18.3	24.1	5.8	19.6
5 5/6/71	18.4 (16.2-19.6)	4.3 (3.4- 4.8)	170	12.5	12.9	21.3	26.2	4.9	14.8
				12.2	12.7	19.7	24.8	5.1	16.3
				12.2	12.5	21.5	26.5	5.0	14.9
				12.2	12.7	20.0	25.6	5.6	17.5
	19.0 (16.0-20.2)	9.7 (9.1-10.6)	170	12.3	12.8	20.7	27.6	6.9	20.3
				12.3	12.8	20.3	26.2	5.9	18.2
				12.1	12.9	19.6	26.8	7.2	22.3
				12.5	12.9	21.7	27.9	6.2	17.8
6 5/26/71	17.7 (16.2-18.4)	4.9 (3.2- 5.2)	100	11.7	12.1	17.9	22.9	5.0	17.6
				11.9	12.6	19.0	25.9	6.9	22.0
				11.8	12.5	19.0	25.4	6.4	20.5
				11.6	12.2	17.3	23.9	6.6	22.9
	18.5 (15.9-19.2)	9.4 (9.2- 9.8)	100	12.1	12.9	20.1	28.8	8.7	25.3
				11.9	12.6	19.6	27.9	8.3	25.0
				11.8	12.6	19.8	29.4	9.6	27.9
				11.6	12.3	17.1	23.9	6.8	23.5
7 9/ 3/70	18.2 (15.4-20.2)	5.1 (4.2- 6.2)	240	11.4	12.7	20.3	27.6	7.3	21.7
				11.5	12.8	20.7	28.5	7.8	22.7
				11.5	12.4	19.3	26.7	7.4	22.9
				11.6	12.5	20.5	26.9	6.4	19.2
	19.0 (15.6-21.8)	9.3 (8.9-10.1)	240	11.9	13.5	21.2	33.3	12.2	32.0
				11.7	13.3	18.8	32.5	13.7	38.2
				11.4	13.0	18.6	29.7	11.1	32.7
				11.4	13.2	21.0	30.6	9.6	26.6
8 6/15/71	23.0 (18.3-25.5)	4.0 (3.0- 4.6)	170	11.4	12.1	16.6	22.0	5.4	19.8
				11.2	12.0	15.1	22.8	7.7	29.1
				11.3	12.2	16.1	22.7	6.6	23.6
				11.4	12.2	16.3	23.3	7.0	25.3
	23.6 (19.4-25.8)	9.0 (8.5- 9.3)	170	11.2	12.6	16.0	26.7	10.8	36.0
				11.1	12.0	14.4	21.7	7.6	28.9
				11.2	12.1	15.1	22.1	7.0	26.9
				11.1	12.3	15.1	26.2	11.1	38.6
9 7/3/71	27.2 (21.4-30.1)	4.2 (3.2- 4.7)	170	11.2	11.9	15.4	20.9	5.5	21.6
				11.2	11.9	16.3	23.1	6.7	24.4
				11.2	12.4	15.3	23.3	8.0	29.4
				11.1	12.2	15.7	24.0	8.2	29.8
	27.6 (20.7-31.4)	8.4 (7.4- 9.1)	170	10.8	12.5	14.2	25.3	11.1	40.2
				11.0	12.1	15.2	23.2	8.0	29.8
				10.9	12.6	14.6	25.6	11.0	39.1
				11.0	12.9	15.5	28.8	13.3	42.8
10 7/24/71	26.5 (22.0-31.6)	5.8 (4.0- 6.6)	170	10.8	11.8	13.7	20.3	6.6	27.6
				10.9	12.1	14.9	24.0	9.1	33.3
				10.7	11.7	14.0	20.0	6.0	25.2
				10.8	12.6	14.1	24.2	10.1	37.7
	26.8 (21.3-32.7)	8.3 (7.8- 9.2)	170	11.0	12.5	15.6	25.6	10.0	34.7
				11.0	12.5	13.8	22.7	8.8	34.5
				10.8	12.4	14.2	22.8	8.6	33.2
				11.1	13.1	13.8	27.4	13.6	47.0

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Table 8. Initial and final densities, and sample weights and caloric values of mosquitofish used in the pond experiments and estimated food consumption rates of bass.

Experiment number and date	Prey density (g/pond)			Food consumption rate of bass (mg/g/day)	Initial Sample			Final sample		
	Initial	Final	Difference		wet (g)	dry (g)	caloric (cal/g dry wt)	wet (g)	dry (g)	caloric (cal/g dry wt)
1 10/13/70	170	123	47	36	5.0	1.34	5746	5.02	1.31	5463
	170	127	43	36				5.07	1.34	5545
2 11/18/70	170	113	57	46	5.0	1.38	5518	5.0	1.30	5020
	170	113	57	48				5.0	1.31	5094
3 9/25/70	170	115	55	46	5.0	1.32	5594	5.0	1.34	5661
	170	106	64	51				5.0	1.36	5571
4 4/12/71	170	119	51	47	11.65	1.93	4784	10.86	1.81	4934
	170	107	63	56				11.06	1.86	4824
5 5/ 6/71	170	124	46	35	11.29	2.05	4921	11.06	1.97	4947
	170	106	64	48				11.15	2.00	5026
6 5/26/71	100	47	53	44	13.25	2.89	5053	11.74	2.61	5127
	100	26	74	57				12.37	2.68	5072
7 9/ 3/70	240	154	86	66	5.1	1.28	5206	5.0	1.18	5248
	240	117	123	85				5.2	1.36	5216
8 6/15/71	170	94	76	70	13.39	3.08	5112	10.31	2.57	5087
	170	73	97	89				11.74	2.89	5139
9 7/ 3/71	170	96	74	69	13.87	3.17	5167	14.15	3.53	5136
	170	69	101	96				14.26	3.57	5118
10 7/24/71	170	90	80	79	14.44	3.97	5182	14.43	4.06	5214
	170	72	98	89				16.62	4.37	5286

Table 9. Statistical comparison between the growth rate values of bass reared at high and low dissolved oxygen levels in the experimental ponds. All values are based on wet weights.

Experiment number and date	Mean dissolved oxygen (mg/1)	Mean temperature (C)	Initial prey density (g/pond)	Mean growth rate[1] (mg/g/day)	Reduction in growth rate (%)	Standard error of the mean	Variance	T[2] value
1	4.2	13.3	170	11.3	0	1.15	5.31	0.01
10/13/70	10.1	13.3	170	11.3		1.25	6.27	
2	5.7	13.3	170	11.1	6	0.56	1.26	0.56
11/18/70	10.3	13.9	170	11.8		1.15	5.36	
3	4.7	16.0	170	15.5	20	0.60	1.47	3.76
9/25/70	9.6	16.5	170	19.4		0.81	2.64	
4	6.0	16.6	170	16.8	14	0.55	1.21	2.50
4/12/71	10.0	16.8	170	19.5		0.91	3.34	
5	4.3	18.4	170	15.9	20	0.61	1.72	3.12
5/6/71	9.7	19.3	170	19.7		1.02	4.19	
6	4.9	17.7	100	20.7	18	1.17	5.45	3.16
5/26/71	9.4	18.5	100	25.4		0.90	3.25	
7	5.1	18.2	240	21.6	33	0.85	2.89	4.27
9/25/70	9.6	19.0	240	32.4		2.36	22.40	
8	4.0	23.0	170	24.4	24	1.91	14.69	2.41
6/15/71	9.1	23.6	170	32.6		2.75	30.35	
9	4.2	27.2	170	26.3	31	1.98	15.83	3.37
7/3/71	8.4	27.6	170	38.0		2.83	32.14	
10	5.8	26.5	170	31.0	17	2.80	31.45	1.49
7/24/71	8.3	26.8	170	37.3		3.22	41.53	

[1] Statistical samples consisted of the growth rate values of the 4 bass from each of the two experiment ponds.

[2] One-tailed T-table value at 95% confidence level with 6 degrees of freedom = 1.943.

Table 10. Initial and final weights, growth rates and biomass of juvenile chinook salmon held in laboratory streams and confronted with different food densities at different oxygen concentrations and temperatures.

Stream	Mean D.O. (mg/l)	Wet weight[1/] (g) Initial	Wet weight[1/] (g) Final	Wet weight[1/] (g) Difference	Dry weight[1/] (g) Initial	Dry weight[1/] (g) Final	Dry weight[1/] (g) Difference	Mean Growth rate[2/] (mg/g/day) Wet	Mean Growth rate[2/] (mg/g/day) Dry	Individual growth rate[3/] (mg/g/day) Dry				Wet biomass Benthos (g/m^2)	Wet biomass Drift (mg/m^3)	Wet biomass Fish (g/m^2)
Experiment 1, 9.5C, 2 fish, 10 days, April 8, 1970																
N3	11.0	1.42	1.99	0.56	.239	.386	.147	33.2	46.9	45.9	48.4	-	-	2.3	4.7	1.10
N6	11.0	1.42	1.89	0.48	.238	.361	.123	28.7	41.0	39.2	43.1	-	-	2.9	3.4	1.07
S4	11.0	1.40	1.92	0.52	.235	.392	.157	31.4	50.0	53.1	46.9	-	-	5.2	6.2	1.07
N1	5.3	1.41	1.86	0.45	.236	.349	.113	27.6	38.7	35.3	42.7	-	-	2.0	0.5	1.05
N4	5.2	1.44	1.92	0.48	.242	.373	.131	28.5	42.5	45.7	38.4	-	-	4.7	0.9	1.08
S5	5.0	1.43	1.97	0.54	.240	.437	.193	31.7	57.3	60.4	53.7	-	-	4.4	7.6	1.10
N2	3.2	1.42	1.82	0.40	.238	.336	.098	24.9	34.1	31.8	36.0	-	-	0.8	2.7	1.04
N5	3.3	1.44	1.84	0.40	.241	.346	.105	24.3	35.8	44.4	48.2	-	-	3.6	1.3	1.09
S6	3.3	1.42	1.61	0.19	.238	.301	.063	12.7	23.3	31.8	12.7	-	-	2.8	3.4	0.98
Experiment 2, 9.8C, 4 fish, 10 days, April 21, 1970																
N3	11.0	3.91	4.44	0.53	.728	.819	.091	12.6	11.8					4.2	2.3	2.83
N6	11.0	3.82	4.51	0.68	.711	.782	.071	16.4	9.5					3.9	1.7	2.90
S4	11.0	3.83	3.93	0.10	.711	.684	-.027	2.7	- 3.8					5.0	1.2	2.49
N1	5.1	4.07	4.07	0.73	.756	.881	.125	16.5	15.3					2.7	3.1	2.86
N4	5.8	3.86	3.86	0.50	.719	.777	.058	12.2	7.8					4.0	2.5	2.65
S5	5.4	3.86	3.86	0.81	.717	.868	.151	18.9	19.0					8.9	3.9	2.75
N2	3.9	4.07	4.70	0.63	.758	.851	.093	14.3	11.6					3.8	2.5	2.83
N5	3.7	3.88	5.12	0.72	.722	.866	.144	16.0	18.1					4.8	3.7	2.90
S6	3.8	3.87	3.74	-0.14	.720	.634	-.086	- 3.6	-12.7					2.3	0.7	2.45
Experiment 3, 11.6C, 2 fish, 10 days, May 8, 1970																
N3	10.5	1.82	2.48	0.66	.318	.471	.153	30.8	39.9	37.5	39.6	-	-	5.1	9.3	1.38
N6	10.5	1.65	2.37	0.72	.288	.474	.186	36.2	48.8	47.7	50.2	-	-	5.2	2.8	1.29
S4	10.5	2.09	2.83	0.74	.366	.522	.156	30.1	35.1	34.5	35.8	-	-	6.7	1.9	1.58
N1	4.7	1.89	2.55	0.66	.331	.494	.163	29.8	39.5	33.3	44.6	-	-	2.9	4.9	1.43
N4	4.8	2.10	2.75	0.65	.367	.525	.158	27.0	35.4	41.3	31.0	-	-	3.1	2.7	1.56
S5	5.8	1.59	2.30	0.71	.278	.451	.173	36.2	47.4	42.2	51.9	-	-	8.1	2.1	1.25
N2	3.6	1.81	2.39	0.58	.316	.449	.133	27.8	34.7	39.4	29.8	-	-	6.1	12.1	1.35
N5	4.2	1.73	2.27	0.54	.302	.421	.118	26.9	32.6	28.6	38.5	-	-	4.5	2.5	1.29
S6	4.0	2.04	2.49	0.46	.356	.469	.113	20.1	27.4	36.6	16.4	-	-	4.0	1.7	1.46

Table 10. Continued

Stream	Mean D.O. (mg/l)	Wet weight[1] (g)			Dry weight[1] (g)			Mean Growth rate[2] (mg/g/day)		Individual growth rate[3] (mg/g/day)				Wet biomass		
		Initial	Final	Difference	Initial	Final	Difference	Wet	Dry	Dry				Benthos (g/m^2)	Drift (mg/m^3)	Fish (g/m^2)
Experiment 4, 13.5C, 2 fish, 10 days, May 25, 1970																
N3[4]	10.1	2.04	3.09	1.05	.353	.559	.206	41.0	45.2					3.7	1.9	1.65
N6[4]	10.1	2.06	2.68	0.62	.356	.466	.110	26.2	26.8					-	0.7	1.53
S4	10.0	2.06	3.57	1.51	.356	.662	.306	53.5	60.2					5.8	4.5	1.82
N1	5.4	2.03	3.11	1.08	.352	.563	.211	42.0	46.1					2.8	4.0	1.66
N4	5.0	2.00	2.78	0.78	.346	.490	.144	32.7	34.4					2.7	2.4	1.54
S5	5.7	2.06	3.40	1.34	.356	.647	.291	49.0	57.9					5.1	4.9	1.77
N2[5]	3.8	1.48	2.07	0.59	.256	.383	.127	33.2	39.1					4.6	2.3	1.14
N5	4.4	1.99	2.50	0.53	.344	.441	.097	23.0	24.7					5.7	1.5	1.45
S6	3.3	2.07	2.54	0.47	.358	.440	.082	20.5	20.6					3.7	1.3	1.49
Experiment 5, 15.5C, 4 fish, 10 days, June 30, 1970																
N3	9.8	3.00	4.12	1.12	.545	.761	.216	31.4	33.1	12.4	42.7	32.5	35.2	1.8	1.4	2.29
N6	9.9	3.76	3.54	-0.22	.685	.606	-.079	- 6.5	-12.3	-14.4	-17.0	-11.8	5.8	0.8	1.8	2.36
S4	9.9	3.40	3.99	0.59	.743	.618	.125	16.1	18.4	35.1	13.6	25.6	- 0.6	1.6	10.6	2.38
N1	5.3	3.12	4.02	0.90	.570	.736	.166	25.1	25.4	9.0	25.9	35.3	20.6	2.1	2.6	2.30
N4[5]	5.0	2.42	2.80	0.38	.440	.448	.048	13.9	10.3	5.9	10.2	13.8	-	14.1	2.5	1.67
S5[5]	5.3	2.74	2.53	-0.21	.500	.450	-.050	- 7.9	-10.5	-11.9	-20.2	1.2	-	-	1.7	1.70
N2	3.6	3.02	3.67	0.65	.551	.682	.131	19.5	21.2	12.7	27.2	18.2	20.7	1.1	1.4	2.16
N5	3.8	3.37	3.34	-0.03	.572	.560	-.012	- 0.9	- 2.1	0.0	- 3.5	- 6.2	1.2	1.6	4.7	2.16
S6	3.3	3.08	3.39	0.31	.599	.562	.037	9.5	6.4	5.4	8.3	- 3.6	13.3	2.0	>100.0	2.09
Experiment 6, 10.4C, 4 fish, 20 days, April 29, 1971																
N3	10.6	7.52	7.54	0.02	1.430	1.367	-.063	0.1	- 2.1	- 5.3	- 3.1	- 3.7	2.7	1.2	2.2	4.86
N6	10.6	7.89	7.29	-0.60	1.500	1.274	-.226	- 3.9	- 8.3	-10.0	1.2	-10.9	-13.6	1.4	2.3	4.90
S4	10.5	7.84	7.57	-0.27	1.490	1.326	-.164	- 1.8	- 5.7	- 1.5	-12.1	- 5.9	- 4.4	2.5	1.5	4.97
N2	5.0	7.86	6.59	-1.27	1.494	1.115	-.379	- 8.8	-14.1	-16.6	-14.1	-16.0	-11.1	3.7	0.5	4.66
N4	4.0	7.44	6.92	-0.52	1.414	1.226	-.188	- 3.6	- 6.8	- 8.1	- 9.9	- 5.9	- 4.8	2.2	4.3	4.63
S5	4.8	7.98	7.59	-0.39	1.517	1.373	-.144	- 2.5	- 5.2	- 7.5	- 0.1	- 3.1	- 1.9	1.7	1.5	5.02
N1	3.0	8.10	6.95	-1.15	1.540	1.206	-.334	- 7.6	-11.9	-13.3	- 9.9	-12.3	-13.7	2.2	2.8	4.92
N5	3.7	8.00	8.00	0.00	1.521	1.457	-.064	0.0	- 2.0	- 4.6	- 1.2	-11.3	5.8	1.1	2.5	5.16
S6	2.6	7.77	7.98	0.21	1.477	1.435	-.042	1.3	- 1.4	0.1	- 4.3	- 0.1	- 1.2	2.2	4.4	5.09

Table 10. Continued

Stream	Mean D.O. (mg/l)	Wet weight 1/ (g)			Dry weight 1/ (g)			Mean Growth rate 2/ (mg/g/day)		Individual growth rate 3/ (mg/g/day)				Wet biomass		
		Initial	Final	Difference	Initial	Final	Difference	Wet	Dry	Dry				Benthos (g/m^2)	Drift (mg/m^3)	Fish (g/m^2)
Experiment 7, 11.0C, 2 fish, 20 days, May 28, 1971																
N3	10.4	3.87	4.23	0.37	.729	.711	-.018	4.5	- 1.3	- 8.7	5.2	-	-	1.0	1.3	2.61
N6	10.4	3.83	4.07	0.24	.743	.737	-.006	3.1	- 0.4	0.5	- 1.4			1.4	1.2	2.55
S4	10.4	3.72	4.43	0.72	.721	.792	.071	8.8	4.7	1.5	7.1	-	-	1.4	1.5	2.63
N2	5.2	3.86	3.51	-0.36	.748	.591	-.157	- 4.8	-11.8	-11.9	-11.4	-	-	0.5	1.3	2.38
N4	4.7	3.75	4.16	0.41	.739	.735	-.004	5.2	- 0.3	- 8.4	6.2	-	-	1.4	1.7	2.32
S5	5.0	3.73	3.75	0.02	.723	.630	-.093	0.2	- 7.0	- 9.6	- 4.8	-	-	1.7	0.4	2.41
N1	3.2	3.87	4.23	0.37	.750	.644	-.006	4.5	- 0.4	- 1.1	0.3	-	-	0.9	1.4	2.61
N5	3.2	3.87	4.01	0.14	.751	.729	-.022	1.8	- 1.5	- 4.2	1.2	-	-	1.0	1.1	2.54
S6	2.8	3.73	3.89	0.16	.724	.683	-.043	2.1	- 3.0	- 6.3	0.0	-	-	0.5	0.9	2.46
Experiment 8, 14.3C, 2 fish, 20 days, July 8, 1971																
N3 4/	9.8	1.24	2.48	1.24	.243	.558	.315	33.3	39.3	39.3	-	-	-	2.6	5.5	2.18
N6	9.8	2.32	4.12	1.80	.452	.885	.433	28.0	32.4	32.5	32.2	-	-	2.9	12.8	2.07
S4	9.8	2.38	4.52	2.14	.484	.927	.443	31.0	31.3	33.9	29.0	-	-	2.0	43.6	2.22
N2	4.9	2.40	4.81	2.41	.468	1.033	.565	33.4	37.6	34.4	39.7	-	-	1.7	7.2	2.33
N4	5.2	2.37	3.09	0.72	.462	.646	.393	13.0	16.6	18.6	14.3	-	-	2.1	8.5	1.76
S5	5.1	2.61	4.79	2.18	.508	1.030	.522	29.5	33.9	35.4	32.4	-	-	3.0	8.9	2.39
N1	3.1	2.64	3.99	1.35	.514	.877	.363	20.5	26.1	18.6	31.6	-	-	2.1	4.5	2.13
N5	3.3	2.68	4.31	1.83	.523	.895	.372	23.3	26.2	27.3	25.3	-	-	2.5	5.3	2.25
S6	3.1	2.66	3.68	1.02	.519	.804	.325	16.1	21.5	18.7	24.4	-	-	1.8	3.3	2.05
Experiment 9, 13.1C, 2 fish, 27 days, August 10, 1971																
N3	10.5	3.18	2.17	-1.10	.668	.345	-.323	-15.2	-23.6	-24.1	-23.3	-	-	2.9	1.1	1.72
N6	10.6	3.32	2.68	-0.64	.697	.505	-.192	- 8.9	-11.8	-16.7	- 6.9	-	-	2.0	2.2	1.94
S4	10.5	3.27	3.14	-0.13	.686	.532	-.154	- 1.5	- 9.4	-13.5	- 6.6	-	-	2.2	0.8	2.07
N2	5.1	3.46	3.02	-0.44	.727	.461	-.266	- 5.0	-16.6	-23.8	- 9.9	-	-	1.5	0.8	2.09
N4	5.0	3.39	2.77	-0.62	.712	.457	-.256	-13.5	-16.2	-21.1	-11.8	-	-	1.7	2.5	1.03
S5	5.1	3.30	3.75	0.46	.692	.632	-.060	4.8	- 3.4	- 1.8	- 5.5	-	-	1.8	1.0	2.27
N1	3.1	3.38	2.84	-0.54	.709	.488	-.221	- 6.4	-13.7	-10.4	-19.4	-	-	1.0	1.2	2.01
N5	3.1	3.18	3.52	0.35	.667	.606	-.061	3.8	- 3.6	- 6.4	- 1.3	-	-	3.2	8.4	1.97

1/ Total weight of all salmon in each stream.

2/ Mean growth rates are expressed as tissue gained or lost in milligrams per mean gram of tissue in each stream ($\frac{\text{final weight plus initial weight}}{2}$) per day.

3/ Individual growth rates are expressed as tissue gained or lost in milligrams per mean gram of tissue ($\frac{\text{final weight plus initial weight}}{2}$) per day.

4/ One salmon trapped in export sample for up to 48 hours.

5/ One salmon was not recovered at end of test period.

Table 11. Statistical evaluation of the growth rates of coho salmon held at high, intermediate, and low dissolved oxygen levels in laboratory streams. Only experiments in which growth rates appeared dependent on dissolved oxygen concentration were compared. All values are based on dry weights.

Experiment number	Mean dissolved oxygen (mg/l)	Mean growth rate (mg/$\bar{g}$/day)	Least significant difference[2]	
			(.05)	(.10)
1	3.3	34.2		*
	5.2	46.1		
	11.0	45.2	11.33	9.33
3	3.9	30.6		*
	5.1	42.8		
	10.5	39.5	9.47	7.70
8	3.2	24.3	*	*
	5.1	29.1		
	9.8	34.4	8.6	7.1

[1] Mean values were calculated from six fish (two in each of the three replicate streams) held at each of three dissolved oxygen levels. Therefore any variance between the replicate streams contributed to the error within each oxygen level.

[2] Asterisk indicates growth rate value significantly different from that of salmon held at near air saturation.

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